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journal homepage: www.elsevier.com/locate/forecoSoil CO₂ efflux in an Afromontane forest of Ethiopia as driven by seasonality and tree speciesYonas Yohannes^{a,b,*}, Olga Shibistova^{a,c}, Asferachew Abate^a, Masresha Fetene^d, Georg Guggenberger^a^a Institute of Soil Science, Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Germany^b Forestry Research Center, Ethiopian Institute of Agricultural Research, P.O. Box 41957, Addis Ababa, Ethiopia^c VN Sukachev Institute of Forest, SB-RAS, Akademgorodok, 660036 Krasnoyarsk, Russian Federation^d Department of Biology, Addis Ababa University, P.O. Box 1176, Addis Ababa, Ethiopia

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ABSTRACT

Variability of soil CO₂ efflux strongly depends on soil temperature, soil moisture and plant phenology. Separating the effects of these factors is critical to understand the belowground carbon dynamics of forest ecosystem. In Ethiopia with its unreliable seasonal rainfall, variability of soil CO₂ efflux may be particularly associated with seasonal variation. In this study, soil respiration was measured in nine plots under the canopies of three indigenous trees (*Croton macrostachys*, *Podocarpus falcatus* and *Prunus africana*) growing in an Afromontane forest of south-eastern Ethiopia. Our objectives were to investigate seasonal and diurnal variation in soil CO₂ flux rate as a function of soil temperature and soil moisture, and to investigate the impact of tree species composition on soil respiration. Results showed that soil respiration displayed strong seasonal patterns, being lower during dry periods and higher during wet periods. The dependence of soil respiration on soil moisture under the three tree species explained about 50% of the seasonal variability. The relation followed a Gaussian function, and indicated a decrease in soil respiration at soil volumetric water contents exceeding a threshold of about 30%. Under more moist conditions soil respiration is tentatively limited by low oxygen supply. On a diurnal basis temperature dependency was observed, but not during dry periods when plant and soil microbial activities were restrained by moisture deficiency. Tree species influenced soil respiration, and there was a significant interaction effect of tree species and soil moisture on soil CO₂ efflux variability. During wet (and cloudy) period, when shade tolerant late successional *P. falcatus* is having a physiological advantage, soil respiration under this tree species exceeded that under the other two species. In contrast, soil CO₂ efflux rates under light demanding pioneer *C. macrostachys* appeared to be least sensitive to dry (but sunny) conditions. This is probably related to the relatively higher carbon assimilation rates and associated root respiration. We conclude that besides the anticipated changes in precipitation pattern in Ethiopia any anthropogenic disturbance fostering the pioneer species may alter the future ecosystem carbon balance by its impact on soil respiration.

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1. Introduction

Despite of the general concern that tropical forests, and particularly intact African forests may play an important role as a carbon sink in the global terrestrial carbon cycle (Ciais et al., 2009; Lewis et al., 2009; Stephens et al., 2007), the size of the carbon stocks and the carbon fluxes in these ecosystems still remain highly uncertain, especially with respect to potential effects of climate change and anthropogenic disturbances.

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Soil CO₂ efflux is one of the largest components in the terrestrial carbon budget (Raich and Schlesinger, 1992), with the global magnitude in the order of 98 Pg C per year (Bond-Lamberty and Thomson, 2010). Contributing more than 50% to the ecosystem respiration across variety of biomes (Janssens et al., 2001; Schlesinger, 1997; Shibistova et al., 2002), soil respiration determines the ecosystem carbon balance and thus an ecosystem sink or source activity (Valentini et al., 2000). Yet to date there has only been a limited amount of data available on soil efflux and its abiotic and biotic determinants for Eastern Africa (Werner et al., 2007) and, likewise, comparative studies across major ecosystems are scarce (Bahn et al., 2010).

Among the climatic conditions controlling soil respiration in different ecosystems on hourly, weekly and seasonally scale, soil temperature and soil moisture are considered to be the two most

influential parameters (Davidson et al., 1998; Reichstein et al., 2003; Rustad et al., 2000). While the relationship between soil CO₂ efflux and soil temperature often is described by a simple exponential function (Davidson et al., 2000; Lloyd and Taylor, 1994; Qi et al., 2002), there is no common agreement on the type of relation between soil moisture and soil respiration. For example, working in an old-growth neotropical forest in Costa Rica, Schwendenmann et al. (2003) found a parabolic relation, while Kosugi et al. (2007), working in a Southeast Asian lowland rain forest, identified a linear dependence of soil CO₂ efflux on soil moisture. Epron et al. (2004) used an exponential regression to fit a relation between soil water content and the seasonal variability of soil respiration. Strong effect of soil moisture on temporal pattern of soil respiration has been shown in some tropical forests and plantations (e.g., Epron et al., 2004; Hashimoto et al., 2004; Kosugi et al., 2007; Ohashi et al., 2008), but just a weak (Salimon et al., 2004) or even no correlation (Adachi et al., 2006) between soil temperature and soil respiration in primary and secondary forests has been reported. In a tropical plantation of New French Guiana, Bréchet et al. (2009) showed no significant relationship between soil respiration and both, soil temperature and soil moisture on a seasonal scale.

Spatial variability of soil CO₂ efflux is primarily affected by biotic factors. So Bréchet et al. (2009) stated that variability of soil respiration was mainly explained by leaf litterfall. Oscar (2007) emphasised the role of different tree species and noted that their different fine root production explained much of the spatial variability in soil CO₂ efflux. Leaf and total aboveground litter (leaf, bark and woody debris) have also been reported to have an effect on soil respiration (Epron et al., 2004).

In this context, long term measurements of soil CO₂ efflux with concurrent climatic record are needed to understand the influence of abiotic and biotic drivers on the magnitude of soil CO₂ efflux. Here, we report on seasonal and diurnal pattern of soil respiration measured underneath a natural mixed evergreen-deciduous Afromontane forest, growing in Ethiopia, East Africa. The Munessa Shashemene forest is one of the largest Afromontane forests in the country. The soil organic carbon pool (0–60 cm depth) of the forest is appreciably high (134 Mg ha⁻¹) and is within the range of similar ecosystems (Lemenih and Itanna, 2004). We carried out our studies under three different tree species: *Croton macrostachys* Hochst, *Podocarpus falcatus* (Thumb.) R.Br.ex and *Prunus africana* (Hook. f.) Kalkman. These tree species differ in a variety of traits, such as crown architecture (Bekele-Tesemma et al., 1993), depth and distribution of roots (Fritzsche et al., 2006), and CO₂ assimilation rate and water relation (Fetene and Beck, 2004; Lüttge et al., 2003). The tree species also represent different functional types according to Whitmore (1989). *Croton macrostachys* is a pioneer deciduous tree, while *P. falcatus* and *P. africana* are late successional evergreen trees, the first being coniferous and the second broadleaf. *Podocarpus falcatus* and *P. africana* are among tree species that are locally threatened by extinction as a result of illegal cutting and encroachment. Such activities created gaps that favor the abundance of the pioneer tree species *C. macrostachys* and diverse shrubs at the expense of climax species. This anthropogenically driven change in relative abundance of tree species may bring modifications in the stand-level carbon balance.

The objective of the present study was, first, to analyze seasonal and diurnal variation in soil CO₂ flux rate as a function of soil temperature and soil moisture. Since Ethiopia is characterized by a strong seasonality of precipitation, we assume soil moisture as the major abiotic driving factor. As a second objective, we were addressing the impact of different functional-type forest tree species on soil CO₂ efflux. Here, we hypothesised that soil CO₂ efflux under deciduous pioneer *C. macrostachys* shows a larger seasonal variability than that under the late successional tree species.

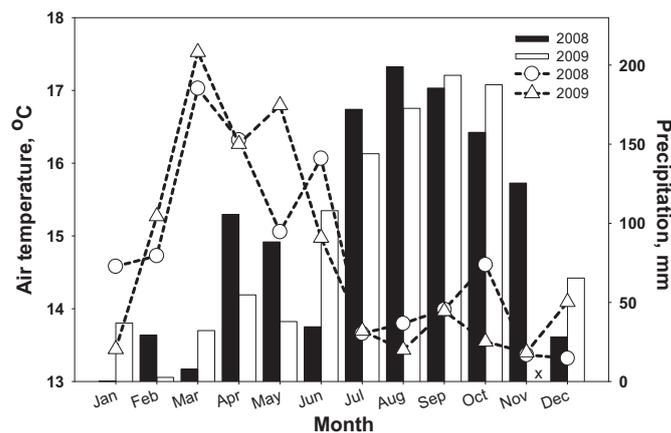


Fig. 1. Monthly total precipitation (bar graph) and mean monthly air temperature (line graph) for the years 2008 and 2009 measured at the Kuke field station being adjacent to the experimental plots (data from Strobl et al., unpublished). x shows missed data in November 2009 due to rain gauge failure.

2. Materials and methods

2.1. Study site

The Munessa–Shashemene forest is located in Oromia Regional State on the eastern escarpment of the southern Main Ethiopian Rift Valley, about 240 km south of Addis Ababa. The forest area, 23,000 ha in size, is divided into three blocks; namely Gambo, Sole and Degaga. For the present study, the experimental plots were established in the Degaga block (07°25'51"N and 038°51'52"E). The elevation is at 2266–2279 m above sea level. Mean annual temperature is 15 °C and mean annual precipitation is about 1200 (data from Ethiopian Meteorological Agency at Degaga town, 07°26'00"N and 038°50'26"E). The study site is located at the central area of the country, with a minor rainy season occurring from March to May and a major rainy season from July to November (Griffits, 1972). Own meteorological records since 2001 show that 80% of the annual precipitation fell in the major rainy season from July to November, and no clear indication of a minor rainy season could be made (Strobl et al., unpublished). Further, the monthly precipitation pattern outside the major rain season varied considerably, e.g. in the years 2008 and 2009 (Fig. 1). Total annual precipitation in both years was similar, with 1133 mm in 2008 and 1036 mm in 2009. Mean annual air temperature corresponded well to the average value, with 14.7 °C in 2008 and 15.3 °C in 2009.

Soils of the study area are rich in clay evolved from volcanic parent material (Fritzsche et al., 2007). At the experimental plots they were classified as Mollic Nitisols according to the WRB system (FAO, 1998). Vegetation of the natural forest is dominated by the canopy species *P. falcatus* and *C. macrostachys*. Other plant species with relatively less abundance include *P. africana*, *Syzygium guineense* (Wild.) DC., *Celtis africana* Burm. f. and *Pouteria adolfi-friederici* (Engl.). The forest is strongly degraded by grazing and illegal logging activities leading to its transformation from a primary to secondary forest.

2.2. Experimental setup and soil CO₂ efflux measurement

Since a major goal of our study was to assess the temporal and spatial variability of the soil CO₂ efflux with respect to the interrelationship of tree species with abiotic factors, the study was carried out on an individual tree basis. In June 2008, for each of the three tree species, *C. macrostachys*, *P. falcatus* and *P. africana*, three individual juvenile trees of the third height class (Tesfaye et al., 2010) were selected. In total, nine experimental plots were

Table 1
Basic characteristic of the soils under the studied trees.

Tree/soil depth	Sand ^a (g kg ⁻¹)	Silt ^a (g kg ⁻¹)	Clay ^a (g kg ⁻¹)	C ^b (g kg ⁻¹)	N ^b (g kg ⁻¹)	pH ^c	CEC ^d (mmol ₍₊₎ kg ⁻¹)	BS ^e (%)	P _{avail} ^f (mg kg ⁻¹)
<i>C. macrostachys</i>									
0–10 cm	211 ± 6	379 ± 20	410 ± 26	138 ± 20	11.7 ± 0.6	6.7 ± 0.04	732 ± 24	100	26 ± 8.5
10–25 cm	219 ± 2	301 ± 24	480 ± 25	64 ± 8	5.9 ± 0.5	6.5 ± 0.44	498 ± 63	100	9.5 ± 5.1
<i>P. falcatus</i>									
0–10 cm	180 ± 3	409 ± 20	411 ± 17	116 ± 11	11.5 ± 0.5	6.5 ± 0.15	565 ± 55	100	15 ± 2.4
10–25 cm	214 ± 4	304 ± 20	482 ± 24	66 ± 13	6.5 ± 0.8	6.2 ± 0.20	376 ± 42	100	8.6 ± 2.4
<i>P. africana</i>									
0–10 cm	195 ± 5	405 ± 37	400 ± 32	122 ± 9	12.2 ± 0.3	6.6 ± 0.13	640 ± 45	100	16 ± 3.0
10–25 cm	222 ± 8	319 ± 27	459 ± 36	80 ± 3	8.2 ± 0.3	6.5 ± 0.16	497 ± 49	100	8.6 ± 0.3

^a Measured by the pipette method (Gee and Bauder, 1986).

^b Total carbon and nitrogen measured by dry combustion (Elementar Vario EL, Hanau, Germany).

^c Analyzed potentiometrically in 1 M KCl [1:2.5 (m/v)].

^d Cation exchange capacity determined with the BaCl₂ compulsive exchange method (Gillman and Sumpter, 1986).

^e Base saturation.

^f Available phosphorus measured after extraction with Bray I (Bray and Kurtz, 1945). Values are mean and standard deviation of three replicated samples.

established, with three replicates for each tree species within a distance of about 100 m. For characterization of the soils underneath the canopies, soil samples were collected from each plot before the start of soil CO₂ efflux measurement campaign. Core soil samples (cylindrical steel core with 4.0 cm diameter) were obtained separately in triplicate from 0–10 and 10–25 cm depths under the canopy of each experimental tree. Soil samples collected under the canopies of same tree species were bulked. According to Table 1, the soil under *C. macrostachys* tends to have a higher pH, appears to be richer in organic carbon and nitrogen, and has a larger cation exchange capacity and more available phosphorus than that under the other tree species. The better soil nutritional status under *C. macrostachys* is likely due to the larger nutrients content in its leaves as compared to the other two tree species (Zech, unpublished). With litter fall, the nutrients are returned to the topsoil.

To assess the seasonal and diurnal variation of soil CO₂ efflux, five permanent soil collars (20 cm in diameter and 5 cm long) made from PVC were inserted in the soil at randomly selected positions underneath the canopy of each individual tree. To minimize any influence of mechanical disturbance of soil surface on diffusion rates, and to avoid cutting of fine roots, the soil collars were inserted into the soil not more than 2 cm. The collars were sealed at the outside with fine sand. Herbaceous understory vegetation was avoided during collar set-up. However, when, in the following two years period, any vegetation grew inside the collars, it was clipped back. Once inserted, soil collars were left in place throughout the measurement period.

Soil CO₂ efflux from the forest floor was measured using an Infrared Gas Analyzer (Li-8100, LI-COR, Lincoln, NE, USA) supplied by a LI-8100-103 Soil Survey Chamber. For each measurement, the soil respiration chamber was placed on each collar, and CO₂ flux rate was automatically calculated from exponential regression of increasing CO₂ concentration over the 2–3 min following chamber equilibration. For each of the tree species mean CO₂ efflux rates were calculated from the 15 chamber measurements obtained during individual sampling events. The measurements began on July 11, 2008 and have been carried out on a weekly basis between 12:00 h and 15:00 h until July 24, 2010 with the exception of October–November, 2009 due to an instrument failure. No measurements were also taken during or immediately following rainfall. Diurnal soil CO₂ efflux measurements were performed over a 24 h period at a 4 h interval. Three days representing different soil moisture categories were selected: 03 July 2008 (wet season); 06 December 2008 (transition from wet to dry season) and 15 March 2009 (dry season).

Soil temperature (°C) at a depth of 0.1 m was monitored within 10–20 cm distance of each collar simultaneously with soil CO₂ efflux measurements using a thermocouple probe (Li-8100-201) connected to the Li-8100. The volumetric soil water content at 0.06 m depth was measured adjacent to each PVC collar with a theta probe (ML2, Delta-T Device Ltd., Cambridge, UK) at three replicates around the collars (the data is available from May 30, 2009).

At a representative place between the plots air temperature underneath the forest canopy, canopy precipitation and soil moisture data were obtained at a weather station. Temperature was measured continuously using 8-bit temperature sensor (Onset Computer Corporation, Bourne, Massachusetts), while precipitation was measured on weekly basis using five randomly distributed polyethylene funnels with a 120 mm upper diameter. Volumetric soil water content was recorded using frequency-domain reflectometer (ECHO probe, Decagon Devices Inc., Pullman, WA) probe installed at 0.1 m depth.

2.3. Data analysis

We separated dry and wet periods following the approaches of Gibbs and Maher (1967), where the distribution of precipitation events over a long-term record is divided into sections for each ten percent of the distribution. Such rainfall deciles were calculated from ten years historical rainfall data (1998–2007) obtained from a nearby metrological station (Degaga town 07°26'00"N and 038°50'26"E). By definition, the fifth decile is the median, and it is near normal classification of wet and dry periods. According to Gibbs and Maher (1967), we used the fifth decile range as a cut-off for dry and wet period classification. Based on that months with more than 55.2 mm rainfall were defined as wet periods and the drier periods are months that received less than 55.2 mm rainfall. This categorized December 2008 to May 2009, December 2009 and January 2010, and March 2010 as dry months while the other months belonged to the wet seasons.

To account for changes in the environmental variables, soil moisture and soil temperature and their interactions with the tree species over the course of the study periods were analyzed with regression approaches to analysis of variance (ANOVA). A general linear model was fitted with soil CO₂ efflux rate as response, and tree species and season (wet vs. dry) as categorical explanatory variables. Soil moisture and soil temperature were fitted into the model as numerical covariates. The model terms were fitted sequentially and ANOVA (type I sums of squares) was computed leading to *F*-tests for the main effects and interactions. We fitted the covariates sequentially in the order soil moisture then soil temperature.

Homoscedastic residuals were obtained with untransformed values. Statistical differences were significant if the probability of type I error was less than 0.05. On the other hand, to analyze the inter-annual soil CO₂ variability among and between the tree species, we averaged soil CO₂ efflux data over the wet and dry periods for both years of observations. Then the data set was analyzed using a three-way ANOVA, with factor effects (tree species, years of observation (first year vs. second year), and season (wet vs. dry)). When ANOVA results indicated significant difference, Tukey's HSD test was performed.

The data for all measurements with both, soil moisture and soil temperature values available from 30 May 2009 to the end of the experiment, were analyzed using nonlinear regression. The objective of the analysis was to describe the dependence of soil respiration on soil moisture alone and jointly with soil temperature under the three tree species separately. Models were fit using non linear least squares method in R 2-11.0 (R Development Core Team, 2009). The performances of the equation were evaluated by goodness-of-fit measures (Root Mean Square Error (RMSE), and r^2). Since in preliminary graphical analysis, the non-linear relation between soil respiration and soil moisture was prominent, while a potential dependency of soil respiration on soil temperature was only weak, we initially modelled the dependency of respiration on soil moisture by different nonlinear models. The Gaussian model was fitting best for all three species both in terms of maximal r^2 values and fitting the downturn of soil respiration rates for high soil moisture values (Eq. (1)). After fitting the first part, different models for including the effect of soil temperature were added: a linear regression (Eq. (2)), a linear regression including an interaction term for temperature and soil moisture (Eq. (3)). After that the reduction of the residual sums of squares (at costs of additional parameters) were tested using F -tests:

$$SR = a * \exp(-0.5 * ((SM - x_0)/b)^2) \quad (1)$$

$$SR = a * \exp(-0.5 * ((SM - x_0)/b)^2) + c * ST \quad (2)$$

$$SR = a * \exp(-0.5 * ((SM - x_0)/b)^2) + c * ST + d * ST * SM \quad (3)$$

where SR is soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), SM is soil moisture (%), ST is soil temperature ($^{\circ}\text{C}$) and a , b , c , d , and x_0 are fitted parameters. To describe the relationships between soil respiration rate (SR) and soil temperature (ST) at a diurnal scale, a single exponential function (Eq. (4)) was used:

$$SR = a * \exp^{b*ST} \quad (4)$$

Annual soil CO₂ efflux was estimated by extrapolating each weekly measurement to a 7-day period. Where there were missing data due to rainfall incidence or failure of instrument, soil CO₂ efflux was estimated based on the Gaussian relation of soil moisture and soil temperature with soil CO₂ efflux for the different tree species shown in Table 3. Since the linear relation between the volumetric soil water content measured at the weather station and underneath the individual tree species was close ($r^2 = 0.94$ for *C. macrostachys*; $r^2 = 0.93$ for *P. falcatus*; $r^2 = 0.93$ for *P. africana*), the former was used to simulate the latter in cases of gaps.

All graphing and statistical analysis was performed using R 2-11.0 or SigmaPlot version 11 (Systat Software Inc., San Jose, CA, USA).

3. Results

3.1. Seasonal variability of soil CO₂ efflux

Soil CO₂ efflux rates varied between 2 and 7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2). In general, the respiration rates followed changes in the precipitation and the resulting changes in the volumetric soil water

Table 2

Analysis of variance for the net effect of explanatory variable tree species, season, and covariates (soil moisture and soil temperature), and their interaction.

Effect	df	SS	(% SS) ^a	F	p-Value
Tree	2	12.970	8.35	38.516	<0.001
Season	1	59.767	38.49	354.982	<0.001
SM	1	33.494	21.57	198.937	<0.001
ST	1	6.531	4.21	38.792	<0.001
Tree:season	1	1.844	1.18	5.476	0.005
Tree*SM	2	5.488	3.53	16.298	<0.001
Tree*ST	2	0.332	0.21	0.984	0.3776
Season:SM	1	0.332	7.98	73.622	<0.001
Season:ST	1	12.395	3.49	32.387	<0.001
SM*ST	1	2.017	1.29	11.981	<0.001
Residual	89	14.985			

^a % SS indicate increases in multiple r^2 (explained variance) due to the addition of this term. df, degree of freedom; SS, sum of square; SM, soil moisture; ST, soil temperature.

content, which varied considerably between 8% and 39%, being on average 16% and 28% for dry and wet months, respectively. So during rainy periods from July to November 2008, from July to November 2009 and from May to July 2010 (end of observation period) soil CO₂ efflux rates mostly exceeded 4 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Drying out of the soil with the onset of dry periods in December 2008 and December 2009 resulted in a continuous decline in the soil respiration rates. Remarkable is the pronounced response of the soil CO₂ efflux on individual rain events during or at the end of a dry period, e.g. in January or April 2009. Table 2 displays the net effect of tree species, season, the covariates soil moisture and soil temperature, and their interaction on the dependent variable soil CO₂ efflux. The ANOVA shows that seasonal changes exerted the strongest influence on soil CO₂ efflux in the Munessa forest, followed by the covariate soil moisture. Seasonality accounted for 38% of variability, with $F(1, 89) = 354.98$, $p < 0.001$, indicating significant difference in the response variable soil CO₂ efflux in wet and dry periods. Soil moisture explained 22% of the overall variances with $F(1, 89) = 198.93$, $p < 0.001$. There was also a significant interaction effect of soil moisture and seasonal variability on soil CO₂ efflux with $F(1, 89) = 73.62$, $p < 0.001$.

Using the data set available from 30 May 2009, we assessed the dependence of soil CO₂ efflux rate on soil moisture individually under the three different tree species. Under all three tree species soil respiration rates steadily increased with increasing volumetric soil water content threshold level (Fig. 3). After exceeding this threshold, soil respiration decreased with increasing volumetric soil water content. The Gaussian Equation (1) shows that the effect of soil moisture had a significant ($p < 0.05$) relationship with soil CO₂ efflux that explained about 50% for *C. macrostachys*, 56% for *P. falcatus*, and 58% for *P. africana* (Table 3).

In contrast to soil moisture, soil temperature at 0.1 m soil depth did not vary much, ranging from about 15 $^{\circ}\text{C}$ to 20 $^{\circ}\text{C}$. The higher soil temperatures were recorded during the dry periods (Fig. 2). The influence of soil temperature on the overall variation of soil CO₂ efflux was smaller as compared with that of soil moisture and tree species. Considering soil temperature as covariate and incorporated in the general linear model, it explains only 4% of the variability of soil CO₂ efflux (Table 2). This is also mirrored in Fig. 4, showing a high degree of scatter between soil temperature and soil respiration.

We also used the same data set to show the joint effects of soil moisture and soil temperature on soil CO₂ efflux rate. The inclusion of the soil temperature in the data analysis (Eq. (2)) increased the r^2 values only weakly and slightly reduced the RMSE (Table 3). The intercepts of the models with the linear trend of soil temperature terms were slightly lower than those with just soil moisture (Table 3). However, the p Linear test, which compares the addi-

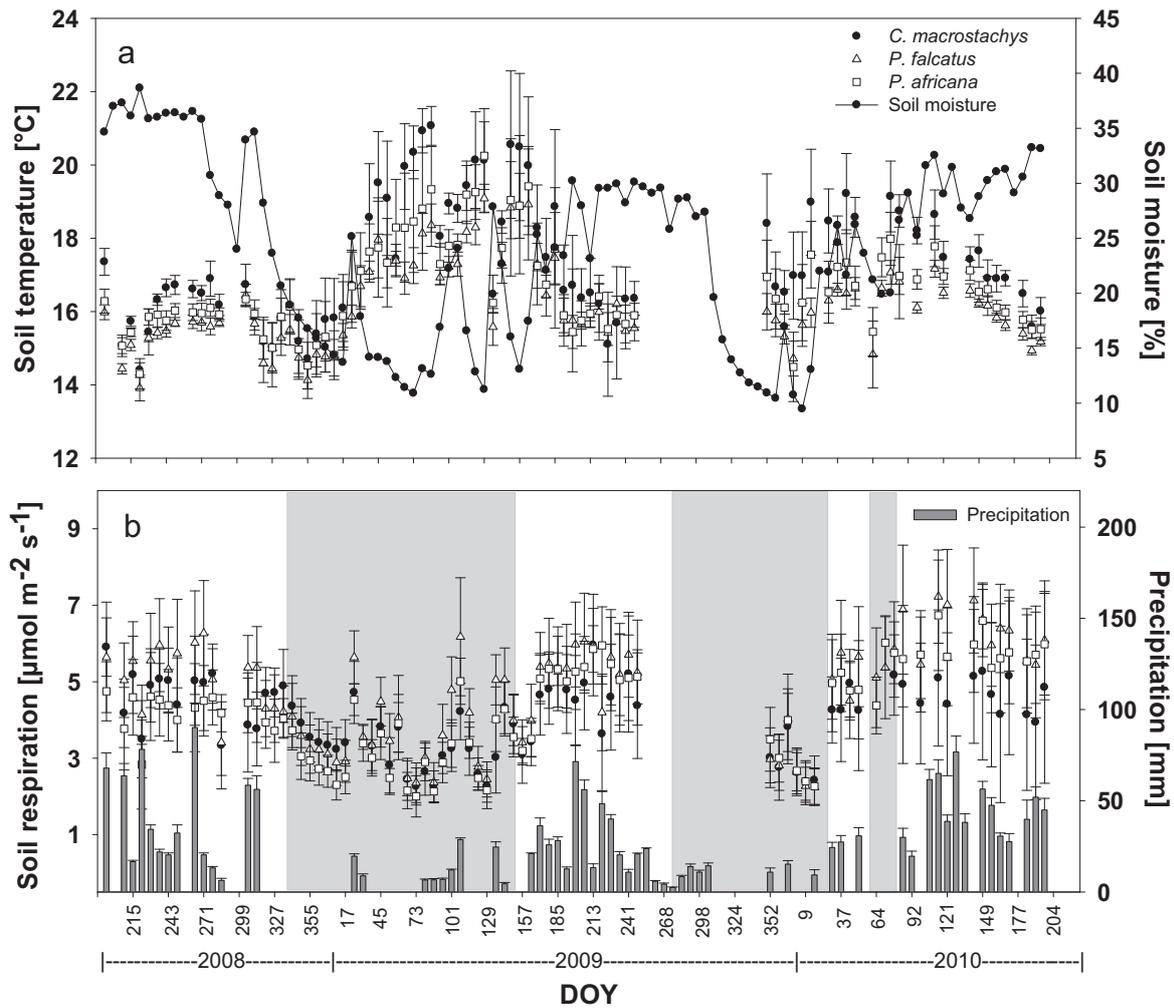


Fig. 2. Seasonal courses of daily mean volumetric soil water content and soil temperature under the canopy (a), weekly canopy precipitation and soil CO₂ efflux rate measured under three tree species (b). Each data point for soil respiration and soil temperature is a mean of fifteen measurements and for precipitation is a mean of five measurements. Error bars indicate standard deviation. Data gaps are due to rain events or instrument failure. Periods with light grey background indicate dry periods as calculated by the approaches of Gibbs and Maher (1967).

tional effects of the linear regression (soil temperature) relative to the previous Gaussian model (soil moisture term in Eq. (1)), was not significant (Table 3). Inclusion of the joint effects of the linear trend depended on soil temperature and the interaction of soil

moisture and soil temperature (Eq. (3)) brought small differences in r^2 and the RMSE values, indicating that the interaction term was more influential than soil temperature alone for *C. macrostachys* ($p < 0.001$) and *P. africana* ($p = 0.002$).

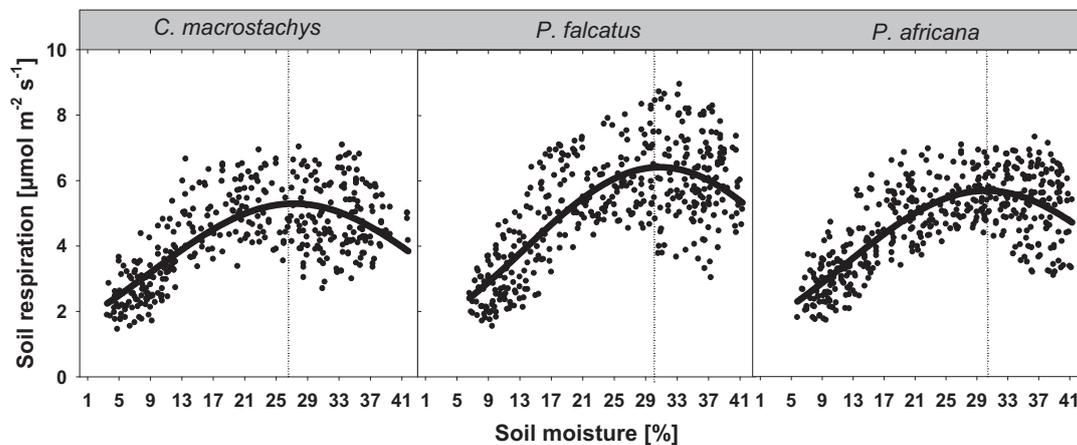


Fig. 3. Relationship between soil CO₂ efflux rate (SR) and volumetric soil water content (SM) at 0.06 m soil depth. The parameters of the Gaussian function (Eq. (1)) are shown in Table 3.

Table 3

Comparative values of regression coefficients, r^2 and RMSE using the Gaussian and a linear regression, a linear regression including an interaction term for soil temperature and soil moisture.

Parameter	<i>C. macrostachys</i>			<i>P. falcatus</i>			<i>P. africana</i>		
	Eq. (1)	Eq. (2)	Eq. (3)	Eq. (1)	Eq. (2)	Eq. (3)	Eq. (1)	Eq. (2)	Eq. (3)
<i>a</i>	5.29	4.84	2.34	6.42	7.32	5.82	5.67	4.91	3.23
<i>b</i>	18.14	11.71	9.88	17.27	18.81	17.90	18.26	16.48	14.31
<i>c</i>	–	0.02	0.03	–	–0.05	–0.137	–	0.05	0.012
<i>d</i>	–	–	0.006	–	–	0.006	–	–	0.0042
x_0	27.27	27.45	18.32	30.60	30.65	24.33	30.28	30.44	24.29
<i>pC</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
<i>pLinear</i>	–	0.3245	–	–	0.1683	–	–	0.0811	–
<i>pLT:T:M</i>	–	–	<0.0001	–	–	0.056	–	–	0.002
<i>pInteraction</i>	–	–	<0.0001	–	–	0.050	–	–	0.002
r^2	0.4975	0.4975	0.5317	0.556	0.558	0.562	0.574	0.577	0.585
RMSE	0.931	0.900	0.900	1.137	1.136	1.132	0.866	0.864	0.856

Eq. (1): $SR = a \cdot \exp(-0.5 \cdot ((SM - x_0)/b)^2)$, Eq. (2): $SR = a \cdot \exp(-0.5 \cdot ((SM - x_0)/b)^2) + c \cdot ST$ and Eq. (3): $SR = a \cdot \exp(-0.5 \cdot ((SM - x_0)/b)^2) + c \cdot ST + d \cdot ST \cdot SM$, where *a*, *b*, *c*, *d* and x_0 are the fitted parameters; r^2 is the correlation coefficient, *SM* is volumetric soil moisture content in %, *SR* is soil respiration in $\mu\text{mol m}^{-2} \text{s}^{-1}$ and *ST* is soil temperature in °C, *pC* (*p* value of complete model), *pLinear* (the linear regression of *ST* relative to the previous model including the Gaussian model for *SM*), *pLT:T:M* (*p*-value for adding a linear trend and a linear interaction for *ST* and *SM* to the Gaussian model fitted with *SM*), *pInteraction* (*p*-value for adding just a linear interaction term *ST:SM* to the Gaussian model with linear regression for *SM*).

3.2. Diurnal variability of soil CO₂ efflux

The volumetric soil water contents in the days representing wet, transition and dry conditions were 26%, 19% and 11%, respectively. The diurnal pattern of the soil temperature was similar for the different seasons, with minima in early morning and maxima in afternoon (not shown). The lowest mean daily soil temperature was recorded under all trees in December, and there were no significant differences in soil temperature for *P. falcatus* and *P. africana* plots between dry and wet seasons (Fig. 5). Under *C. macrostachys*, the soil temperatures were higher as compared to other plots due to the less dense canopy and showed maxima during the dry and sunny March term. The season was exerting a strong influence on the soil CO₂ efflux rates. Largest values were obtained in the July measurement, representing the wet period and optimal soil moisture, while in March the smallest diurnal CO₂ efflux rates were obtained. The impact of the season on temperature dependency of the diurnal CO₂ efflux is also reflected by the Q_{10} values calculated from the exponential function in Fig. 5 (i.e., \exp^{10b}). Q_{10} values of 3.2 for *C. macrostachys*, 4.5 for *P. falcatus*, and 2.7 for *P. africana* during the wet season indicated a higher temperature sensitivity of soil respiration than respective Q_{10} values of 2.0, 1.6, and 2.0 in the transition season. In contrast to wet and transition seasons where the pattern of the soil CO₂ efflux rates followed the diurnal soil temperature fluctuations, no diurnal temperature dependency

of soil CO₂ efflux rates was observed for all the plots in the dry period.

3.3. Tree species variability in soil CO₂ efflux

It has been shown that the tree species was the third significant factor affecting soil CO₂ efflux variability $F(2, 89) = 38.51$, $p < 0.001$ (Table 2). Tree species contributed with 8% to the overall variance. Further, the significant interaction effects of tree species and soil moisture ($p < 0.001$) indicates that the change in soil CO₂ efflux rate as a function of soil moisture was not uniform under the different tree species. This is also obvious from the Gaussian functions (Table 3). The threshold level when higher soil moisture leads to a decline of the soil CO₂ efflux decreased in the order *P. falcatus* (volumetric soil water content 31%), *P. africana* (30%), *C. macrostachys* (27%). Likewise, absolute largest soil respiration rates at optimum soil moisture were observed under *P. falcatus* (Fig. 3). In contrast, it appears that the decrease in soil CO₂ efflux with decreasing soil moisture was least for *C. macrostachys* followed by *P. africana*, while *P. falcatus* exhibited the steepest decline in soil respiration with drying out of the soil. This result is mirrored by the three-way ANOVA showing that soil respiration did vary significantly ($p < 0.05$) between the tree species during wet periods (Fig. 6). In both years under study, the mean soil respiration rate during the wet period

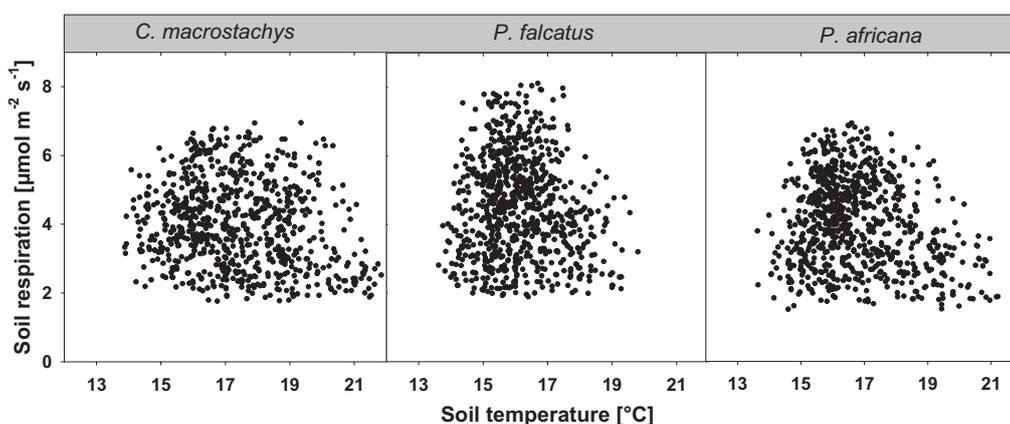


Fig. 4. Relationship between soil CO₂ efflux rate (*SR*) and soil temperature (*ST*) at 0.1 m soil depth.

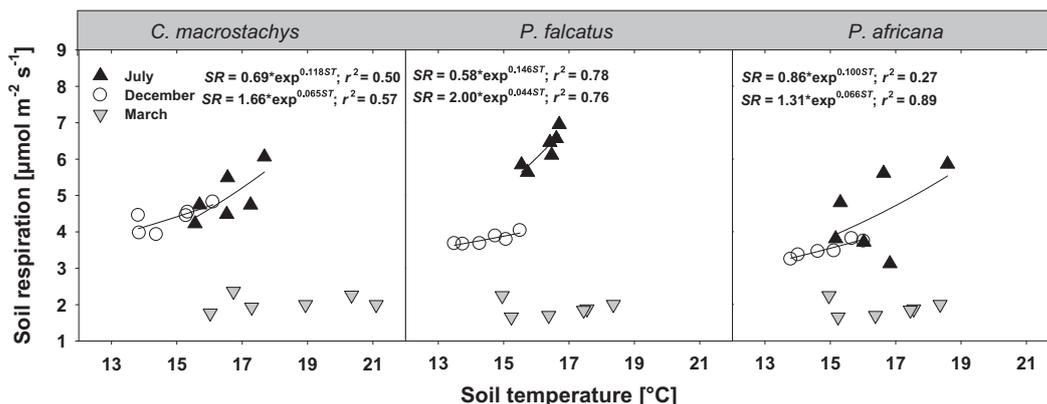


Fig. 5. Diurnal dependence of soil CO₂ efflux rate (SR) on soil temperature (ST) at 0.1 m soil depth. Each data point is the mean of fifteen measurements made per sampling hour. The equations represent July and December measurements, respectively.

was highest under *P. falcatus*. In contrast, there were no significant differences ($p > 0.05$) in the soil CO₂ efflux rate under the three tree species during the dry season.

4. Discussion

4.1. Variability of soil respiration related to soil moisture

Soil respiration under the canopy of all three tree species showed pronounced seasonal variation. It is evident that these seasonal changes are generally driven by the precipitation pattern and its response variable volumetric soil water content. The strong positive relationship between soil moisture and soil respiration is in agreement with previous studies in tropical forest ecosystems where a majority of biological processes coincides with moisture dynamics (e.g., Epron et al., 2004, 2006; Hashimoto et al., 2004; Nsabimana et al., 2009; Salimon et al., 2004; Werner et al., 2007). In general, the highest soil respiration rate during the wet periods may have resulted from the high physiological activity of both plants and microorganisms (Lee et al., 2002) in not limiting soil moisture conditions. Besides this general effect of soil moisture on soil respiration rates, rewetting of the soil after dry periods causes a short-lived but strong increase in soil CO₂ efflux. This observation is known as “Birch effect” and is the result of burst mineralization of labile soil organic matter that has been accumulated during the dry period and is available to microor-

ganisms after re-wetting of the soil (Birch, 1964; Jarvis et al., 2007).

At our study, volumetric soil water content was positively related to soil CO₂ efflux rates only when it was below around 30%, at higher values there appeared a negative relation. Since volumetric soil water contents of up to 42% were measured, soil respiration rates were below the maximum values under these wet conditions. Excess soil moisture may negatively affect CO₂ efflux rates by reducing soil aeration and thus CO₂ diffusivity (Janssens and Pilegaard, 2003). Oxygen deficit as result of too high soil moisture decreases activity of plant roots (Adachi et al., 2006) and the heterotrophic decomposition of soil organic matter (Linn and Doran, 1984). This may be particularly the case in the clayey soils under study. An alternative explanation is based on the photosynthetic activity of the trees. The periods with the most amount of precipitation are associated with conditions of low photosynthetic active radiation in the Munessa forest with c. 1–4 mol m⁻² leaf area d⁻¹ (Seyoum et al., in preparation). This translates to small carbon assimilation rates and, consequently, to small rates of autotrophic soil respiration.

4.2. Variability of soil respiration related to soil temperature

We examined possible seasonal effects of soil temperature on soil respiration and found little relation for the investigated forest ecosystem. The apparent weak contribution of soil temperature unlike to soil moisture is partly due to the relatively small temperature fluctuations in this ecosystem being not sufficient enough to drive seasonal variations in soil respiration. Further, soil temperature tended to be higher during the dry periods when soil CO₂ efflux was restrained by low soil moisture. Similar observations have been found in other tropical forest ecosystem where soil temperature is relatively constant within the year and poorly correlated with soil respiration (e.g., Davidson et al., 2000; Hashimoto et al., 2004; Kiese and Butterbach-Bahl, 2002; Nsabimana et al., 2009). In other biomes such as boreal and temperate forests, there is a wide range of seasonal temperatures that leads to seasonal variation in soil respiration rate (Davidson et al., 1998; Malhi et al., 1999; Shibistova et al., 2002).

Over diurnal pattern, when soil moisture is assumed to be almost constant, soil temperature is considered to be a major control of soil CO₂ efflux (e.g., Chang et al., 2008). Also we found a positive relation between soil temperature and soil respiration, as long as soil moisture is not limiting as is the case at the July and December measurements. The Q₁₀ values suggest that the more favorable is the soil moisture the more prominent is the tem-

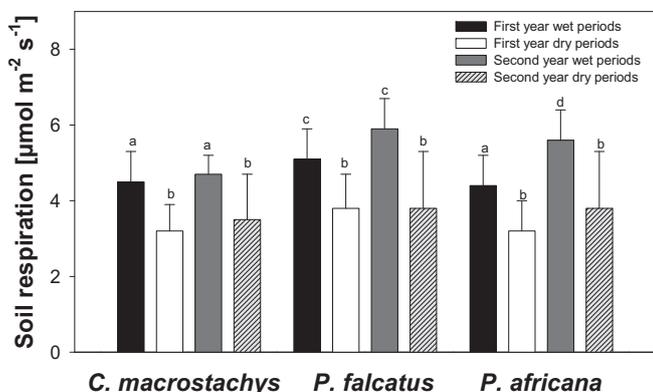


Fig. 6. Comparison of soil CO₂ efflux between wet and dry periods for both years of observation (July 11, 2008 to July 10, 2009 and July 11, 2009 to July 17, 2010). Bar graphs following a different letter are significantly different (Tukey's HSD, $p < 0.05$). Error bars indicate standard deviation.

perature dependency of the diurnal soil CO₂ efflux. This may be attributed to increasing soil organic matter mineralization rates with increasing temperature. But according to Tang et al. (2005), largest soil respiration rates in the afternoon rather suggest that biotic processes, coupled to photosynthesis, carbon allocation to roots and autotrophic may control diurnal CO₂ efflux.

4.3. Effects of trees on soil CO₂ efflux

Our analysis demonstrated that different tree species affected soil respiration. At optimum soil moisture, the soil CO₂ efflux under *P. falcatus* exceeded that under the other two tree species (Fig. 3). Several biotic factors such as assimilation rate, root density, phenological differences, soil microbial activity and diversity (Epron et al., 2006; Raich and Tufekcioglu, 2000; Vanhala, 2002) might explain this observation. During the wet season with dominantly clouded sky, the shade tolerant *P. falcatus* is having a physiological advantage as compared with the light demanding *C. macrostachys* in terms of carbon assimilation (Seyoum et al., in preparation). So it seems reasonable that the higher soil respiration rate during the wet period under the canopy of *P. falcatus* than under the other two tree species is associated with the cumulative metabolic activities of the plant.

The situation changes when the dry season is progressing. With decreasing soil moisture, soil respiration decreased under all three tree species, however, the change in magnitude of soil CO₂ efflux rate under *P. falcatus* was larger than under *C. macrostachys* and *P. africana*. The least soil moisture sensitivity was observed for *C. macrostachys*. Probably, this reflects the different sensitivity of the three tree species on soil moisture. Seyoum et al. (in preparation) analyzed particularly larger values of carbon assimilation and transpiration for *C. macrostachys* than for the other two tree species during the dry season. This pronounced photosynthetic activity of *C. macrostachys* during the dry period probably results in a relative large root respiration, thus causing a less pronounced decline in CO₂ efflux during conditions of low soil moisture than for the other two tree species.

4.4. Annual soil CO₂ efflux

Cumulative annual soil CO₂ efflux was highest under *P. falcatus* with 144 mol m⁻² in the first year and 162 mol m⁻² in the second year of observation. Respective values for *C. macrostachys* were 131 mol m⁻² and 135 mol m⁻², and for *P. africana* 140 mol m⁻² and 156 mol m⁻². With that the cumulative annual soil CO₂ efflux falls within the range of other published estimates of secondary tropical forests in eastern Amazon (150 mol CO₂ m⁻² year⁻¹; Davidson et al., 2000), tropical monsoon forests in Thailand (213 mol CO₂ m⁻² year⁻¹; Hashimoto et al., 2004), monospecific forest plantation in Rwanda (112 mol CO₂ m⁻² year⁻¹, Nsabimana et al., 2009), and moist tropical lowland forest in Panama (128 mol CO₂ m⁻² year⁻¹, Sayer et al., 2007). In most studies soil collars were installed randomly over the whole experimental plots. In the present study collars were installed randomly but underneath the canopy of our experimental trees. Wiseman and Seiler (2004) showed that measurement position had significant effect on soil respiration, and soil CO₂ efflux rates were consistently near the trees. This suggested that the estimated annual soil respiration probably reflects a comparatively higher CO₂ efflux rate than at a completely randomized design at the forest ecosystem level.

As shown in Table 2, the season is having the strongest influence on the soil respiration. The mean soil CO₂ efflux rate was higher during the wet period than during the dry period, independently of the study tree and the year of observation (Fig. 6). When the two study years are compared, there were no differences in the soil CO₂ efflux rates neither for the wet period nor for the dry period

(except the second year wet period observation under *P. africana*). However, during the first year of observation six months were classified as dry periods, whereas at the second year only three months fell into this category because of a more homogenous distribution of the precipitation. Hence, the higher soil CO₂ efflux rates during the second year of observation could be related to fewer periods where soil respiration was restrained due to low soil moisture. This shows that the precipitation pattern is having a strong impact on the soil cumulative soil respiration in the Afromontane forest.

5. Conclusions

The soil CO₂ fluxes from soil to atmosphere in the Munessa forest is primarily controlled by soil moisture, and with that by the precipitation pattern. Therefore, the length of dry and wet seasons is of utmost importance for the soil CO₂ efflux and the whole carbon balance of this ecosystem. In Ethiopia, predicted future changes in precipitation pattern are likely to have considerable direct effects on soil CO₂ efflux over most of the year. However, this study also shows that biological variability is an important factor, because different functional types of trees are responding differently on precipitation pattern with respect to soil CO₂ efflux. Since anthropogenic impact to the forest structure, e.g. by changes in the intensity of grazing-induced disturbance, favors the pioneer *C. macrostachys* at the cost of the late successional tree species, this adds another important driving factor in the seasonal and annual variability of soil respiration at local scales. Interestingly the late successional *P. falcatus* shows a larger variability in soil CO₂ efflux rates than the pioneer *C. macrostachys* that colonizes disturbed niches.

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