Does soil moisture overrule temperature dependency of soil respiration in Mediterranean riparian forests?

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Abstract

Soil respiration (SR) is a major component of ecosystem’s carbon cycle and represents the second largest CO₂ flux of the terrestrial biosphere. Soil temperature is considered to be the primary control on SR whereas soil moisture as the secondary control factor. However, soil moisture can become the dominant control on SR in very wet or dry conditions. Determining the trigger that switches-on soil moisture as the primary control factor of SR will provide a deeper understanding on how SR changes under projected future increased droughts. Specific objectives of this study were (1) to investigate the seasonal variations and the relationship between SR and both soil temperature and moisture in a Mediterranean riparian forest along a groundwater level gradient; (2) to determine soil moisture thresholds at which SR is rather controlled by soil moisture than by temperature; (3) to compare SR responses under different tree species present in a Mediterranean riparian forest (Alnus glutinosa, Populus nigra and Fraxinus excelsior). Results showed that the heterotrophic soil respiration rate, groundwater level and 30 cm integral soil moisture (SM₃₀) decreased significantly from riverside to uphill and showed a pronounced seasonality. SR rates showed significant differences among tree species, with higher SR for P. nigra and lower SR for A. glutinosa. The lower threshold of soil moisture was 20 and 17 % for heterotrophic and total SR respectively. Daily mean SR rate was positively correlated with soil temperature when soil moisture exceeded the threshold, with Q₁₀ values ranging from 1.19 to 2.14; nevertheless, SR became decoupled from soil temperature when soil moisture dropped below these thresholds.

1 Introduction

Soil is the largest pool of terrestrial organic carbon in the biosphere, storing around 2344 Pg C in the top 3 m (Jobbágy and Jackson, 2000). Soil respiration (SR) is the main carbon efflux from ecosystems to the atmosphere, accounting for 60–90 % of the total ecosystem respiration. Thus, SR plays an important role in the global carbon bal-
ance (Schimel et al., 2001; Raich et al., 2002), and even small changes of SR may induce positive feedbacks to climate change (Schlesinger and Andrews, 2000). Therefore, it is critical to have a good understanding on how SR interacts with environmental conditions.

Previous studies have shown that SR is very sensitive to soil temperature and soil moisture (Fang and Moncrieff, 2001). Soil temperature has been recognized as the most important factor controlling SR because it affects the respiratory enzymes of both roots and soil microbial biomass (Xu et al., 2011). In general, SR increases exponentially with increases of soil temperature (Epron, Daniel et al., 1999; Lloyd and Taylor, 1994; Mielnick and Dugas, 2000). In contrast to the positive relationship between SR and soil temperature, both very high and very low soil moisture has been shown to diminish the temperature response of SR (Londo et al., 1999; Welsch and Hornberger, 2004) due to the potential oxygen limitations under high soil moisture (Skopp et al., 1990) and due to metabolic drought stress under very low soil moisture (Orchard and Cook, 1983). Soil moisture also affects the plant composition and productivity (Häring et al., 2013) and thus, controls the quantity and quality of both soil organic matter (SOM) and root exudate supply (Rustad et al., 2000).

Most of the long-term global modelling studies consider soil temperature as the sole parameter to predict SR rates. However, in Mediterranean and semiarid ecosystems, SR is highly sensitive to soil moisture and the temperature-driven increases in SR are likely dampened by low soil moisture (Conant et al., 2004; Raich and Potter, 1995; Rey et al., 2002). Therefore, using alone soil temperature is clearly insufficient to properly describe SR patterns. In addition, though there are already many studies of how soil temperature and soil moisture affect SR, the switch from temperature to soil moisture as the primary control factor of SR remains unclear.

SR can be divided into autotrophic and heterotrophic respiration by different biological sources (Hanson et al., 2000). Autotrophic respiration, also known as root respiration, is mainly dependent on tree physiology such as photosynthesis substrate supply (Heinemeyer et al., 2007; Hogberg et al., 2001). Heterotrophic respiration is the sum of
microbial decomposition of SOM (Fang et al., 2005; Knorr et al., 2005). In theory, due to the different origins of autotrophic and heterotrophic respiration, they may have different sensitivities toward environmental factors and respond differently to seasonality (Epron et al., 2001; Kuzyakov and Larionova, 2006; Yan et al., 2010).

Riparian areas represent higher soil moisture and more sustained water tables (McGlynn and Seibert, 2003). In these ecosystems, tree species composition and tree growth is strongly influenced by the topographic position concomitant with the changes in the soil water content. Thus, this may indirectly affect SR through litter input and nutrient availability. Because of the retardation of microbial decomposition with the frequent saturation of soil water, riparian areas tend to accumulate more SOM than hillslope areas do (Sjögersten et al., 2006).

The main objectives of this study were: (1) to investigate the seasonal variations and relationships between SR and both soil temperature and moisture in a Mediterranean riparian forest along a groundwater level gradient; (2) To determine soil moisture thresholds at which SR is rather controlled by soil moisture than by temperature, even in such non-water stressed environments; (3) To compare SR responses under different tree species present in a Mediterranean riparian forest (Alnus glutinosa, Populus nigra and Fraxinus excelsior). With these aims, we carried out measurements of SR under different tree species along a groundwater level gradient in a riparian forest in NE Spain. The results of our study may help to better understand the interactions between different components of SR with soil temperature and moisture, as well as the role of different tree species. It also provides relevant information for SR model's parameterization.
2 Material and methods

2.1 Site description

The experiment was conducted in a riparian forest growing along Font de Regàs stream, a headwater tributary of La Tordera river, in Montseny Natural Park (North of Barcelona; 41°50’ N, 2°30’ E, altitudinal range 300–1200 m a.s.l.). The forest community of our study site consists of black alder (Alnus glutinosa L.), black locust (Robinia pseudoacacia L.), common ash (Fraxinus excelsior L.), and black poplar (Populus nigra L.). As a result of water and nutrient availability, A. glutinosa and P. nigra are mostly distributed nearby the river whereas F. excelsior are located further away on the upper site, near to the hill. R. pseudoacacia trees are scattered over the study area and were not monitored. Mean annual temperature is 12 °C with maximum and minimum average temperatures of 10 and 14 °C, respectively. The mean annual precipitation is 872 mm (1951–2010). The riparian soil is sandy-loam with low rock content (< 13 %), weakly acid (pH of 6.7), and has an average bulk density of 1.09 g cm⁻³.

2.2 Experimental design

We divided the groundwater gradient (riparian-hillslope transect) into 4 levels according to the distance from the riverside and tree species composition (Fig. 1). The distances of level 1 to level 4 (L1 to L4) from the river centre were 2.7, 4.4, 6.8 and 11.8 m, respectively. The three target tree species, A. glutinosa, P. nigra and F. excelsior were located at level L1, L2 and L3, respectively. To examine the interaction effects on SR of tree species, soil moisture and temperature, we set three transects crossing the riparian-hill to measure the variation of total SR (sum of soil autotrophic and heterotrophic respiration, hereafter referred to collectively as total SR, \( \text{SR}_{\text{tot}} \)) from different tree species. Soil chambers were placed 1.5 m from the stem of the target tree species. Moreover, we also set two transects to measure the topographic effects on soil heterotrophic respiration (\( \text{SR}_H \)). Due to the difficulty of trenching next to the riverbank, chambers for \( \text{SR}_H \)
were set only at level L2, L3 and L4. To separate root respiration from SR\textsubscript{H}, we inserted a PVC tube (diameter: 65 cm, height: 40 cm) into the soil five months before starting the measurements. To avoid constraints on groundwater table level fluctuations by the PVC tube, we cut two opposite windows on the PVC tube and covered by 65 µm mesh to prevent root growth through the windows.

Stainless-steel rings were inserted permanently into the soil, down to 3 cm depth, as the base of the soil chambers, and kept free from seedlings throughout the experiment duration. The distances of each soil chamber from the riverside varied slightly due to the tree distribution.

### 2.3 Field measurement

SR and soil temperatures were measured seasonally from summer 2011 to autumn 2012. These measurements were conducted continuously for one week within each season. A heavy rainfall event took place in winter 2012, resulting in elevated water levels of the river that washed away most of the litter layer within three meters distance from the river bank.

\( \text{CO}_2 \) concentration was measured in situ with an automatic changeover open system. The system consists of an infrared gas analyzer (IRGA, LiCor 6262, LiCor, Inc., Lincoln, NE, USA), a datalogger (CR10, Campell Scientific Inc., UT, USA), 12 pairs of channels, 12 soil chambers, 12 pairs of rotameters, 6 pumps and two flowmeters. Each pair of channels consists of two tubes connected to a soil chamber, one attached on the top of chamber (reference \( \text{CO}_2 \) concentration) and another attached at the base for calculating the increment of \( \text{CO}_2 \) concentration provided by SR. Soil chambers were placed from the beginning of each field campaign and \( \text{CO}_2 \) concentrations were analysed and recorded sequentially over 1 min interval at each chamber. Air was continuously forced through all chambers by pumps. Only one chamber at a time was connected to the IRGA to analyse the \( \text{CO}_2 \) concentration of the respective chamber, while air from the others was exhausted to the atmosphere until their own turn. The sequence was programmed every four 4 cycles of differential IRGA measurements from 12 cham-
bers, and an additional cycle of absolute IRGA measurement, which was then used to calculate the actual absolute ambient air concentration of CO$_2$ in ppm. The CO$_2$ concentration of the ambient air was determined as the difference between the scrubbed sample, which flows through soda lime and Mg(ClO$_4$)$_2$ and the ambient air sample.

Soil chambers were protected by placing a 50 cm $\times$ 50 cm green fine mesh on top to avoid possible heating by direct sun light during the measurements. Soil temperature of 5 cm depth was continuously measured with Pt100 temperature sensors and recorded in parallel with the CO$_2$ concentration analysis. Thirty cm integral soil moisture (cm$^3$ cm$^{-3}$, SM$_{30}$) in each level were determined and recorded half-hourly with moisture reflectometer (CS616, Campbell Scientific). Additionally, we also measured 5 cm integral soil moisture (SM$_5$) next to each soil chamber once per day during each measuring field campaign, with impedance probes (Delta-T Theta Probe Soil Moisture Sensor, MI2x, Delta-T Devices, Cambridge, England). A grid of 28 wells (PVC tubes of 35 mm in diameter) was installed to monitor groundwater table oscillation. Wells were distributed along the study site and at different distances from the stream: 2.7, 4.4, 6.8, 11.8 m ($n=7$). Groundwater levels were monitored manually every two weeks using a sounding device with acoustic and light signal (Eijelkamp, Agrisearch Equipment). In autumn of 2012, after concluding the measurements, litter layer and soil samples (15 cm depth) inside each chamber were collected. Litter layer samples were weighted after oven-drying at 65–70 $\degree$C for 24 h. Soil samples were first oven-drying at 105 $\degree$C and then analyzed to determine their organic carbon and nitrogen content by using Walkley–Black method and Kjeldahl method, respectively.

### 2.4 Statistical analysis

Statistical analyses were performed with PASW statistics 18 (SPSS Inc., 2009, Chicago, IL). The missing data of soil temperatures were estimated from air temperature values based on a regression analyses between air and soil temperatures. SR, soil temperature and soil moisture data were analyzed using ANOVA to examine whether seasonal SR rates were different among levels and tree species. Data used to test the
significance in ANOVA were based on daily means. Least significant difference (LSD) was used to detect differences among levels and tree species for each season. We used regression analysis to examine the relationship between SR and soil temperature. An univariate exponential equation was fitted (van’t Hoff, 1898)

\[ SR = ae^{bT} \]  

where \( SR \) is soil respiration rate (\( \mu \text{mol C m}^{-2} \text{s}^{-1} \)), \( T \) is soil temperature (°C), \( a \) is basal respiration and \( b \) is the temperature sensitivity of SR. A \( Q_{10} \) value for the whole measurements period was computed for each topographic position and tree species on the basis of daily average SR rate and soil temperature. In addition, we estimated specific \( Q_{10} \) values for summer of 2011 and 2012. Data collected were fitted to the exponential equation. The apparent \( Q_{10} \) was calculated as:

\[ Q_{10} = e^{10b} \]  

In order to understand the interaction between soil temperature and soil moisture and the effect of soil moisture on regulating SR, we applied recursive partitioning analysis to search for the threshold of soil moisture. As models based on partitioning can only handle linear models, the equation above was transformed by linearizing with logarithms:

\[ \ln SR = \ln a + bT \]  

Logarithmic transformed SR values were used as the dependent variable. Once the soil moisture thresholds were obtained, linear and nonlinear regression analyses were used to determine the relationship between SR, soil temperature and soil moisture in each soil moisture interval. The recursive partitioning analysis was conducted in the \( R \) statistical environmental using the \textit{party} package (Zeileis et al., 2008).
3 Results

3.1 Seasonal variation of groundwater level, soil moisture and soil temperature

Seasonal variation of air temperature and precipitation was remarkable. The precipitation in 2011 was significantly higher than in 2012, especially in summer. Summer precipitation in 2011 was four times higher (183 mm) than in 2012 (39 mm). SM30 was significantly higher at L1 (Fig. 2). In summer 2012, due to a remarkable drought, SM30 at L1 only showed a small decrease with respect to summer 2011; while at the other levels (L2, L3 and L4) SM30 was markedly decreased. Groundwater levels showed no seasonal variation but were significantly different among them.

Soil nearby the river contained less organic carbon and nitrogen, but a higher C : N ratio, with a C : N ratio of 12.13 (Table 1). Soil C : N ratio decreased from the riverside to uphill whereas the dry weight of litter layer increased from the riverside to uphill. The largest amount of dry weight of litter layer was found under F. excelsior, and coincided with the highest soil organic carbon (SOC) and soil nitrogen concentration among levels.

3.2 Seasonal variation of SRH along hillslope transect

SRH rates ranged from 0.17 µmol C m\(^{-2}\) s\(^{-1}\) (in winter, L4) to 1.69 µmol C m\(^{-2}\) s\(^{-1}\) (in summer, L2, Fig. 3). SRH decreased significantly from riparian zone (L2) to hill zone (L4), especially in summer. SRH measured from different levels were significantly different in all seasons (P < 0.05). SRH at L2 had a higher variability during the whole experiment. Minimum soil temperature coincided with maximum SM5 in winter while maximum soil temperature was recorded in summer when SM5 was lowest. SRH varied markedly during the year following the change of soil temperature from summer 2011 to spring 2012, and the changes of SM5 for summer and autumn 2012. As expected, SRH was lower during winter when soil temperatures were the lowest of the
year, and SR$_H$ was higher during the growing season. SM$_{30}$ at L2 was significantly lower than SM$_{30}$ at L1, but higher than SM$_{30}$ at L3 and L4.

### 3.3 Tree species effects on SR$_{tot}$

The observed variation of SR$_{tot}$ for the three tree species followed the change of soil temperature over the year (Fig. 3). SR$_{tot}$ of *P. nigra* was the highest one, especially during summer, and SR$_{tot}$ of *A. glutinosa* was the lowest one throughout the year. There were no significant differences of soil temperatures among tree species locations. SM$_5$ did not differ among tree species location but there was a tendency towards a higher SM$_5$ under *F. excelsior*. SM$_{30}$ was significantly different among levels for all seasons. The variation of SM$_{30}$ at L1 was lower and showed less seasonal variability, maintaining most of the SM$_{30}$ values around 40%. During both summers 2011 and 2012, SM$_{30}$ at L3 dropped till around 10%, which is even lower than the SM$_5$ at L4 where *F. excelsior* is found.

### 3.4 Drought and rain pulse effects on SR

The precipitation of 39 mm of summer 2012 was 21% lower than precipitation of summer 2011. This lower precipitation caused a significant reduction of around 50% of SM$_5$, 14–35% of SM$_{30}$ and at the same time a reduction of SR between 21 and 49%. The $Q_{10}$ values ranged from 0.97 to 1.40 in summer 2011 and 0.63 to 1.14 in summer 2012 (Table 2).

A rainfall event (13 mm) during the measurement period of summer 2012 caused a significant increase of soil moisture and SR rates at all levels (L1 to L4). The SM$_5$ increased around 21–74% after the rainfall event even though it only caused a 0–20% increase of the SM$_{30}$ (Table 3). This rainfall event caused a sharply increase of SR from 0.41–0.99 µmol C m$^{-2}$ s$^{-1}$ to 0.59–1.66 µmol C m$^{-2}$ s$^{-1}$, which corresponds to an increase of SR around 34 to 68%.
3.5 The switch of primary control factor of SR

We identified three SM$_5$ intervals for each SR$_H$ and SR$_{tot}$ (Table 4), which suggest the existence of thresholds in soil moisture effect. SR was positively related ($P < 0.001$) to soil temperature when soil moisture was higher than 23% for SR$_H$, or higher than 27% for SR$_{tot}$. The lower threshold for SR$_H$ and SR$_{tot}$ were 20 and 17% of SM$_5$ respectively. Under the low bound value, SR$_H$ showed a significantly positive relation with SM$_5$ (Fig. 4, linear regression with $r^2$ of 0.89, 0.92 and 0.91 for L2, L3 and L4) while SR$_{tot}$ showed a weak positive relation with SM$_5$ (Fig. 5, linear regression with $r^2$ of 0.56, 0.11 and 0.10 for L1, L2 and L3). The exponential model based on soil temperature accounts for 68 to 84% of the variation in both SR$_H$ and SR$_{tot}$ rates at the higher SM$_5$ interval values. The fitted $Q_{10}$ values in high SM$_5$ interval ranged from 1.49 to 2.14. Generally the $Q_{10}$ values of SR$_H$ were lower than the $Q_{10}$ of SR$_{tot}$.

4 Discussion

4.1 Effect of groundwater level and soil moisture on SR

In studies of Martin and Bolstad (2005) and Pacific et al. (2008), it was indicated that the amount and availability of soil water varies depending on landscape position and topography. Both studies also show that small differences in micro-topography appear to be important in driving soil moisture conditions. This is in accordance with our results; the overall seasonal trends of soil moisture were similar, but differences in the relative magnitude of soil moisture still can be found among levels.

In our study site, the SR$_H$ was significantly higher at L2 and decreased with the distance from the river. At the same time, SR$_{tot}$ of A. glutinosa at L1 was significantly lower than the other two species found at L2 and L3. This result could be explained by limitations to SR imposed by groundwater level in two different ways. First, when groundwater level is low, drought stresses soil microbial and root respiration activity,
and secondly when groundwater level is high and close to topsoil surface, it limits soil aeration and likely reduces the effective respiring soil volume. Pacific et al. (2008) showed that the soil CO₂ concentrations were significantly higher in the riparian zone as a result of higher soil moisture. In contrast, Zanchi et al. (2011) found lower SR in plots after drainage, and suggested that the low C and N content in the topsoil near to the river, where most of the soil CO₂ respiration is produced, could partially explain that low SR. The discrepancy of these two studies could be associated to the different drainage regimes, as the poorly drained plots imply an anaerobic inhibition of SR. In our study, however, SR₇ was measured at L2, L3 and L4 under well-drained conditions and SR₇ decreased concomitantly with the decrease in the availability of soil water. Nonetheless, SR₇ of A. glutinosa was measured at L1, where the soils sometimes experienced flooding or not well-drained conditions, and the root respiration may be inhibited by the high groundwater level.

Additionally, landscape position and topography not only altered the availability of soil water but also affected the annual range of soil moisture. This is shown by Zanchi et al. (2011) studying riparian SR in Amazonia. They indicate that riparian soil is very sensitive to the changes of water flooding regime. The high groundwater table in riparian zones implies intermittent anaerobic conditions and diffusion of the inhibition during water saturation. These differences in soil moisture caused by site topography may result in differences in SR even though the soil temperatures were similar among sites. The different behaviours of SR₇ and SR₇ from L1 to L4 from our results indicate a different contribution of SR₇ to SR₇. As the root system of A. glutinosa may constantly experience a saturated water regime, the relative contribution from root respiration may be much lower than the one of the other two species.

4.2 Rain pulse and drought effects on SR

The Mediterranean climate is characterized by summer droughts that affect particularly the top soil layers, therefore rainfall events during these dry periods can trigger abrupt increases in SR for days (Bowling et al., 2011; Cisneros-Dozal et al., 2007; Lee et al., 2002).
Lee et al. (2004) simulated precipitation and found that hardwood forest floors were very sensitive to changes in moisture in the upper soil layers. Moreover, Wang et al. (2012) noted that the response of litterfall respiration is very sensitive to rainfall, and the increase in soil moisture by rainfall primarily enhanced the litterfall respiration but depressed mineral SR. Similar results were published by Casals et al. (2011) reporting that SR after a precipitation pulse was mostly derived from SR$_H$ with a contribution up to 70% of total SR$_{tot}$. Hence, our findings seem to be consistent with these previous studies.

### 4.3 Confounding of temperature and moisture effects on SR

This study aimed at assessing the importance of soil moisture on soil respiration and determining the threshold of soil moisture at which soil moisture overrules temperature in controlling SR. The response of SR to soil moisture has been widely studied and described by various types of functions, such as linear or logarithmic functions depending on the soil type, climate or vegetation type (Comstedt et al., 2010; Epron et al., 1999; Orchard and Cook, 1983). In our study, the seasonal courses of SR$_H$ and SR$_{tot}$ generally followed the seasonal cycle of temperature, but moderated by soil moisture. Such a relationship is in agreement with other previous studies (Davidson et al., 1998; Martin and Bolstad, 2005; Wang et al., 2013).

The positive linear relationship between SR and soil moisture in low soil moisture conditions found in our work agrees with many previous studies where low soil moisture constrains SR (Almagro et al., 2009; Davidson et al., 1998; Keith et al., 1997; Rey et al., 2002; Wang et al., 2013; Xu and Qi, 2001). In our study, the low soil moisture and warmer temperatures actually reduced SR rates, resulting in lower $Q_{10}$ values at the lower soil moisture. A similar decline of $Q_{10}$ with decreasing soil moisture has been reported by Conant et al. (2004), Curiel Yuste et al. (2003) and Wen et al. (2006). Low soil water content not only reduces the contact between substrate and enzymes and microbes, it also decreases the substrate supply due to the increased drying-out of litter and topsoil layer (Davidson et al., 2006). Another possible reason for the
observed lower $Q_{10}$ is that the reduction of photosynthesis decreases the translocation of photosynthates to the rhizosphere (Hogberg et al., 2001; Nordgren et al., 2003).

In a Norway spruce stand, Gärdenäs (2000) found that litter moisture explained most of the variation of SR whereas mineral soil moisture, air or litter temperatures were not significantly affected. Our results showed that the seasonal variations of SR$_H$ and SR$_{tot}$ were mainly controlled by soil temperature, with secondary influence by soil moisture (SM$_5$). Using the recursive partitioning method, we have identified clear thresholds for SM$_5$ effects on the temperature sensitivity of SR. Soil moisture thresholds at which SR temperature sensitivity is reduced have been found in several studies, from different ecosystems (Fang and Moncrieff, 2001; Gaumont-Guay et al., 2006; Jassal et al., 2008; Lellei-Kovács et al., 2011; Palmroth et al., 2005; Wang et al., 2013). However, the threshold values in soil moisture seem to be site specific, as the factors limiting water uptake by plants and microbes may differ among ecosystems. Even in the same climate region, different soil moisture thresholds have been found from previous studies. For example, Almagro et al. (2009) investigated how soil moisture modulated the sensitivity of soil respiration in different ecosystems in the Mediterranean region and found that the threshold value of soil moisture was 10%. Above this soil moisture values, $Q_{10}$ ranged from 1.86 to 2.20 and decreased to 0.44 to 0.63 when soil moisture was lower than 10%. Furthermore, Rey et al. (2002) found in a Mediterranean oak forest that soil temperature accounted for 85% of the variation of SR when soil moisture was above 20% with a $Q_{10}$ value of 2.34. Nonetheless, Xu and Qi (2001) found that with soil moisture higher than 14%, the $Q_{10}$ value was 1.8 and decreased to 1.4 when soil moisture was lower than 14%.

### 4.4 Other factors affecting SR

In addition to soil moisture threshold values, we also found variations of SR$_H$ and SR$_{tot}$ among position and tree species in each soil moisture interval. For example, when SM$_5$ was lower than 20%, SR$_H$ measured at L4 was always lower than SR$_H$ measured at L2 and L3. When SM$_5$ was lower than 17%, SR$_{tot}$ of *P. nigra* was significantly higher than...
for the other two species, suggesting that there are still other factors affecting $SR_H$ and $SR_{tot}$ variations. Several explanations for this result are plausible. First, spatial variability in vegetation can affect SR due to differences in root respiration and the quantity and quality of detritus (Raich and Tufekcioglu, 2000). These biophysical gradients across landscape positions can lead to strong spatial heterogeneity in SR. Tree species in our study site exhibit different litterfall temporal patterns and may also contribute to the seasonal variation of the availability of SOC and nutrients to the microbial community and roots. Second, the vitality of tree species in responses to soil water regime could generate different root respiration rates. Additional data of daily sapflow of the studied trees from our study site (data no shown) confirmed the difference in tree transpiration and growth activity. For example, the water use efficiency of $P. nigra$ was highest, followed by $F. excelsior$ and $A. glutinosa$. Besides, the mean diameter at breast height (DBH) of $P. nigra$ is larger than mean DBH of the other tree species. $P. nigra$ may be more efficient in uptaking water and nutrients compared to the other two tree species.

5 Conclusions

This research demonstrates how soil moisture constrains the relationship between SR and soil temperature. We present critical threshold values of soil moisture where SR dependency on soil moisture overrules soil temperature dependency. Our results also reveal the importance of soil moisture as a predictor of SR even in a non-water-stressed environment such as riparian forests. Our findings provide support for modelling approaches that include soil temperature and soil moisture, by making available parameters to predict SR rates. This study has also implications for a better understanding of global change impacts on the carbon cycle, since soil water availability will likely become an increasingly crucial factor for most terrestrial ecosystems under climate change.
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Table 1. Soil carbon and nitrogen content and litter L and F organic horizons on soil floor dry weight from soil respiration chambers.

<table>
<thead>
<tr>
<th>Groundwater level</th>
<th>C/N</th>
<th>SOC %</th>
<th>NITROGEN%</th>
<th>Litter Layer (kg m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L2 – Near river</td>
<td>10.40</td>
<td>2.73</td>
<td>0.16</td>
<td>0.97</td>
</tr>
<tr>
<td>L3 – Intermediate</td>
<td>10.00</td>
<td>4.38</td>
<td>0.26</td>
<td>1.20</td>
</tr>
<tr>
<td>L4 – Uphill</td>
<td>9.15</td>
<td>3.36</td>
<td>0.23</td>
<td>1.67</td>
</tr>
<tr>
<td>L1 – <em>A. glutinosa</em></td>
<td>12.13</td>
<td>2.29</td>
<td>0.11</td>
<td>0.69</td>
</tr>
<tr>
<td>L2 – <em>P. nigra</em></td>
<td>10.27</td>
<td>3.52</td>
<td>0.20</td>
<td>1.18</td>
</tr>
<tr>
<td>L3 – <em>F. excelsior</em></td>
<td>9.67</td>
<td>4.85</td>
<td>0.30</td>
<td>2.21</td>
</tr>
</tbody>
</table>
Table 2. Comparison of soil respiration rates (SR), soil moistures (SM) and $Q_{10}$ values in 2011 and 2012 summer campaigns. Heterotrophic SR (SR$_{H}$), Total SR (SR$_{tot}$), Five cm integral soil moisture (SM$_{5}$), Thirty cm integral soil moisture (SM$_{30}$).

<table>
<thead>
<tr>
<th>Chamber</th>
<th>SR (µmol C m$^{-2}$ s$^{-1}$)</th>
<th>SM$_{5}$ (%)</th>
<th>SM$_{30}$ (%)</th>
<th>$Q_{10}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SR$_{H}$</td>
<td>L2 – Near river</td>
<td>1.65</td>
<td>0.84</td>
<td>49 %</td>
</tr>
<tr>
<td></td>
<td>L3 – Intermediate</td>
<td>0.98</td>
<td>0.70</td>
<td>28 %</td>
</tr>
<tr>
<td></td>
<td>L4 – Uphill</td>
<td>0.74</td>
<td>0.50</td>
<td>32 %</td>
</tr>
<tr>
<td>SR$_{tot}$</td>
<td>L1 – <em>A. glutinosa</em></td>
<td>1.24</td>
<td>0.78</td>
<td>37 %</td>
</tr>
<tr>
<td></td>
<td>L2 – <em>P. nigra</em></td>
<td>1.42</td>
<td>1.13</td>
<td>21 %</td>
</tr>
<tr>
<td></td>
<td>L3 – <em>F. excelsior</em></td>
<td>1.26</td>
<td>0.76</td>
<td>40 %</td>
</tr>
</tbody>
</table>

All data of SR, SM$_{5}$ and SM$_{30}$ were significantly different between 2011 and 2012. All $p$ values < 0.001.
Table 3. Comparison of soil respiration rates (SR), and soil moistures (SM) after a rainfall event of 13.5 mm in summer 2012. Heterotrophic SR (SR\textsubscript{H}). Total SR (SR\textsubscript{tot}). Five cm integral soil moisture (SM\textsubscript{5}). Thirty cm integral soil moisture (SM\textsubscript{30}). Data were averaged for two days before and two days after the rainfall event.

<table>
<thead>
<tr>
<th>Chamber</th>
<th>SR (µmol C m\textsuperscript{-2} s\textsuperscript{-1})</th>
<th>SM\textsubscript{5} (%)</th>
<th>SM\textsubscript{30} (%)</th>
<th>Increase</th>
<th>Increase</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>before</td>
<td>after</td>
<td>increase</td>
<td>before</td>
<td>after</td>
</tr>
<tr>
<td>SR\textsubscript{H}</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L2 – Near river</td>
<td>0.66</td>
<td>1.00</td>
<td>52 %</td>
<td>14.09</td>
<td>18.84</td>
</tr>
<tr>
<td>L3 – Intermediate</td>
<td>0.59</td>
<td>0.80</td>
<td>34 %</td>
<td>15.19</td>
<td>18.37</td>
</tr>
<tr>
<td>L4 – Uphill</td>
<td>0.41</td>
<td>0.59</td>
<td>45 %</td>
<td>12.06</td>
<td>17.51</td>
</tr>
<tr>
<td>SR\textsubscript{tot}</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L1 – A. glutinosa</td>
<td>0.67</td>
<td>1.04</td>
<td>54 %</td>
<td>11.27</td>
<td>16.91</td>
</tr>
<tr>
<td>L2 – P. nigra</td>
<td>0.99</td>
<td>1.66</td>
<td>68 %</td>
<td>10.86</td>
<td>18.86</td>
</tr>
<tr>
<td>L3 – F. excelsior</td>
<td>0.68</td>
<td>0.98</td>
<td>44 %</td>
<td>11.10</td>
<td>17.20</td>
</tr>
</tbody>
</table>
**Table 4.** Exponential relationships between soil respiration (SR) and soil temperature (T), and $Q_{10}$ for different SM$_5$ intervals. Heterotrophic SR (SR$_H$). Total SR (SR$_{tot}$). (SM$_5$) is 5 cm integral soil moisture.

<table>
<thead>
<tr>
<th></th>
<th>SM$_5$ &gt; 23%</th>
<th>23% &gt; SM$_5$ &gt; 20%</th>
<th>SM$_5$ &lt; 20%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$F_n$</td>
<td>$R^2$</td>
<td>$Q_{10}$</td>
</tr>
<tr>
<td>SR$_H$</td>
<td>L2 – Near river</td>
<td>$0.52e^{0.05T}$</td>
<td>0.77***</td>
</tr>
<tr>
<td></td>
<td>L3 – Intermediate</td>
<td>$0.51e^{0.04T}$</td>
<td>0.72***</td>
</tr>
<tr>
<td></td>
<td>L4 – Uphill</td>
<td>$0.40e^{0.05T}$</td>
<td>0.84***</td>
</tr>
<tr>
<td></td>
<td>SM$_5$ &gt; 27%</td>
<td>27% &gt; SM$_5$ &gt; 17%</td>
<td>SM$_5$ &lt; 17%</td>
</tr>
<tr>
<td>SR$_{tot}$</td>
<td>L1 – <em>A. glutinosa</em></td>
<td>$0.53e^{0.04T}$</td>
<td>0.77***</td>
</tr>
<tr>
<td></td>
<td>L2 – <em>P. nigra</em></td>
<td>$0.52e^{0.05T}$</td>
<td>0.78***</td>
</tr>
<tr>
<td></td>
<td>L3 – <em>F. excelsior</em></td>
<td>$0.32e^{0.08T}$</td>
<td>0.68***</td>
</tr>
</tbody>
</table>

* *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$
Table A1. Analysis of variance (ANOVA) statistics for soil temperature (ST), soil moisture (SM): SM$_5$, SM$_{30}$, and heterotrophic soil respiration (SR$_H$) of different levels of the same season (Mean ± SD). LSD was used to test post hoc. Means with the same letter are not significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Champaign</th>
<th>ST</th>
<th>SM$_5$</th>
<th></th>
<th>SM$_{30}$</th>
<th>SR$_H$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L2</td>
<td>L3</td>
<td>L4</td>
<td>L2</td>
<td>L3</td>
</tr>
<tr>
<td>2011 Summer</td>
<td>16.11 ± 0.73(A)</td>
<td>17.88 ± 0.88(AB)</td>
<td>18.12 ± 2.02(B)</td>
<td>27.11 ± 0.74(A)</td>
<td>31.68 ± 3.20(B)</td>
</tr>
<tr>
<td>2011 Autumn</td>
<td>10.87 ± 0.30(A)</td>
<td>12.48 ± 0.24(B)</td>
<td>13.33 ± 0.25(C)</td>
<td>33.51 ± 4.75(A)</td>
<td>35.33 ± 7.00(A)</td>
</tr>
<tr>
<td>2012 Winter</td>
<td>1.75 ± 1.22(A)</td>
<td>5.13 ± 1.92(B)</td>
<td>6.11 ± 1.50(B)</td>
<td>33.14 ± 4.50(A)</td>
<td>31.21 ± 3.00(A)</td>
</tr>
<tr>
<td>2012 Spring</td>
<td>18.82 ± 1.13(A)</td>
<td>18.81 ± 1.04(A)</td>
<td>20.03 ± 1.25(B)</td>
<td>18.73 ± 4.31(A)</td>
<td>18.87 ± 2.89(A)</td>
</tr>
<tr>
<td>2012 Summer</td>
<td>20.18 ± 2.05(A)</td>
<td>21.70 ± 2.74(A)</td>
<td>20.80 ± 2.40(A)</td>
<td>14.94 ± 4.99(A)</td>
<td>14.91 ± 4.35(A)</td>
</tr>
<tr>
<td>2012 Autumn</td>
<td>7.11 ± 2.58(A)</td>
<td>7.66 ± 3.98(A)</td>
<td>8.73 ± 3.38(A)</td>
<td>26.87 ± 6.08(A)</td>
<td>26.77 ± 5.80(A)</td>
</tr>
</tbody>
</table>
Soil moisture overrules temperature dependency of soil respiration

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Table B1. Analysis of variance (ANOVA) statistics for soil temperature (ST), soil moisture (SM): SM₅, SM₃₀, and total soil respiration (SRₜₒₜ) of different tree species of the same season. LSD was used to test post hoc. Means with the same letter are not significantly different (P < 0.05).

<table>
<thead>
<tr>
<th>Campaign</th>
<th>ST</th>
<th>SM₅</th>
<th>SM₃₀</th>
<th>SRₜₒₜ</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A. glutinosa</td>
<td>P. nigra</td>
<td>F. excelsior</td>
<td>A. glutinosa</td>
</tr>
<tr>
<td>2011 Summer</td>
<td>17.51 ± 1.07(AB)</td>
<td>18.11 ± 1.09(A)</td>
<td>17.04 ± 1.73(B)</td>
<td>27.24 ± 4.67(A)</td>
</tr>
<tr>
<td>2011 Autumn</td>
<td>11.16 ± 0.20(A)</td>
<td>11.11 ± 0.71(A)</td>
<td>11.77 ± 0.69(B)</td>
<td>34.46 ± 4.60(A)</td>
</tr>
<tr>
<td>2012 Winter</td>
<td>2.02 ± 2.00(A)</td>
<td>3.00 ± 2.49(A)</td>
<td>2.05 ± 4.17(A)</td>
<td>31.24 ± 3.42(AB)</td>
</tr>
<tr>
<td>2012 Spring</td>
<td>18.16 ± 0.84(A)</td>
<td>18.53 ± 0.64(A)</td>
<td>18.57 ± 1.48(A)</td>
<td>16.19 ± 2.80(A)</td>
</tr>
<tr>
<td>2012 Summer</td>
<td>19.74 ± 1.69(A)</td>
<td>22.15 ± 3.11(B)</td>
<td>19.57 ± 2.07(A)</td>
<td>34.46 ± 4.60(A)</td>
</tr>
<tr>
<td>2012 Autumn</td>
<td>7.08 ± 2.27(AB)</td>
<td>8.71 ± 2.49(A)</td>
<td>6.07 ± 4.15(B)</td>
<td>23.80 ± 3.53(A)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Campaign</th>
<th>L1</th>
<th>L2</th>
<th>L3</th>
<th>A. glutinosa</th>
<th>P. nigra</th>
<th>F. excelsior</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011 Summer</td>
<td>42.49 ± 0.45(A)</td>
<td>22.22 ± 0.23(B)</td>
<td>12.60 ± 0.36(C)</td>
<td>1.24 ± 0.28(A)</td>
<td>1.42 ± 0.33(A)</td>
<td>1.26 ± 0.20(A)</td>
</tr>
<tr>
<td>2011 Autumn</td>
<td>42.92 ± 3.52(A)</td>
<td>28.69 ± 2.20(B)</td>
<td>12.60 ± 3.32(C)</td>
<td>0.69 ± 0.27(AB)</td>
<td>0.89 ± 0.22(B)</td>
<td>0.80 ± 0.04(A)</td>
</tr>
<tr>
<td>2012 Winter</td>
<td>46.08 ± 0.11(A)</td>
<td>27.35 ± 0.22(B)</td>
<td>18.61 ± 0.18(C)</td>
<td>1.44 ± 0.08(A)</td>
<td>0.28 ± 0.08(A)</td>
<td>0.26 ± 0.04(B)</td>
</tr>
<tr>
<td>2012 Spring</td>
<td>37.62 ± 0.10(A)</td>
<td>21.91 ± 0.41(B)</td>
<td>14.17 ± 0.51(C)</td>
<td>0.85 ± 0.14(A)</td>
<td>1.10 ± 0.17(A)</td>
<td>1.16 ± 0.29(B)</td>
</tr>
<tr>
<td>2012 Summer</td>
<td>36.58 ± 0.63(A)</td>
<td>14.51 ± 0.07(B)</td>
<td>9.22 ± 0.78(C)</td>
<td>0.78 ± 0.17(A)</td>
<td>1.13 ± 0.43(B)</td>
<td>0.76 ± 0.31(A)</td>
</tr>
<tr>
<td>2012 Autumn</td>
<td>40.76 ± 0.50(A)</td>
<td>27.27 ± 1.12(B)</td>
<td>20.38 ± 1.03(C)</td>
<td>0.49 ± 0.17(A)</td>
<td>0.81 ± 0.14(B)</td>
<td>0.68 ± 0.12(C)</td>
</tr>
</tbody>
</table>
Soil moisture overrules temperature dependency of soil respiration

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Figure 1. Sketch of levels in a gradient of soil water availability with tree species distribution and $SR_H$ chamber positions.
Figure 2. Seasonal changes of summer 2011 (Su11), autumn 2011 (Au11), winter 2012 (Wi12), spring 2012 (Sp12) and autumn 2012 (Au12) in (a) mean seasonal air temperature and precipitation; (b) 30 cm integral soil moisture (SM$_{30}$); (c) groundwater level, value represents the depth of groundwater level from soil surface (L1, L2, L3 and L4).
Figure 3. Seasonal changes of summer 2011 (Su11), autumn 2011 (Au11), winter 2012 (Wi12), spring 2012 (Sp12) and autumn 2012 (Au12) in (A–D). Data of soil heterotrophic respiration rates (SR_H). (A) SR_H along groundwater level gradient. (B) 5 cm soil temperature. (C) 5 cm integral soil moisture (SM_5). (D) 30 cm integral soil moisture (SM_30). (E–H) Data of total soil respiration rates (SR_tot) of three tree species. (E) SR_tot under different tree species. (F) 5 cm soil temperature. (G) 5 cm integral soil moisture (SM_5). (H) 30 cm integral soil moisture (SM_30). All values are mean ± SD. Data points marked with * indicate significant differences among species at P ≤ 0.05 (Detail please refer to Appendix A and B).
Figure 4. Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factor for $SR_H$. (A) At $SM_5 \geq 23\%$, positive correlations of $SR_H$ with soil temperature in all levels. (B) At $20\% \leq SM_5 < 23\%$, transition with no clear relationship of neither SM nor ST with $SR_H$. (C) At $SM_5 < 20\%$, no relationship between SR and ST as the inset figure shows, it switches from ST to $SM_5$ as controlling factor with positive correlations between $SR_H$ and $SM_5$ for all levels. Campaigns with $SM_5 < 20\%$ were all from spring and summer 2012. $SM_5$ (5 cm integral soil moisture)
Figure 5. Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factor for SR$_{\text{tot}}$. (A) At SM$_5 \geq 27\%$, positive correlations of SR$_{\text{tot}}$ with soil temperature under all tree species. (B) At $17\% \leq \text{SM}_5 < 27\%$, positive but slightly weaker correlations of SR$_{\text{tot}}$ with soil temperature under all tree species. (C) SM$_5 < 17\%$, no relationship between SR and ST as the inset figure shows, it switches from ST to SM$_5$ as controlling factor with positive correlations between SR$_{\text{tot}}$ and SM$_5$ for all tree species. Campaigns with SM$_5 < 17\%$ were all from spring and summer 2012. SM$_5$ (5 cm integral soil moisture)