**1** # Does soil moisture overrule temperature dependency of

**2** # soil respiration in Mediterranean riparian forests?

**3**

**4** **Chao-Ting Chang[1,2], Santiago Sabaté[1,2], Dominik Sperlich[1,2], Sílvia**

**5** **Poblador[2], Francesc Sabater[2] and Carlos Gracia[1,2]**

**6**

**7** [1]{Centre for Ecological Research and Forestry Applications (CREAF), Universitat

**8** Autonoma de Barcelona, 08193 Bellaterra, Barcelona, Spain}

**9** [2]{Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Diagonal

**10** 645, 08028 Barcelona, Spain}

**11**

**12** Correspondence to: C.T.Chang (Chaoting@creaf.uab.es)

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**14** **Abstract:**

**15** Soil respiration (SR) is a major component of ecosystem's carbon cycle and represents

**16** the second largest $CO_2$ flux of the terrestrial biosphere. Soil temperature is considered

**17** to be the primary abiotic control on SR whereas soil moisture as the secondary control

**18** factor. However, soil moisture can become the dominant control on SR in very wet or

**19** dry conditions. Determining the trigger that switches-on soil moisture as the primary

**20** control factor of SR will provide a deeper understanding on how SR changes under

**21** projected future increased droughts. Specific objectives of this study were (1) to

**22** investigate the seasonal variations and the relationship between SR and both soil

**23** temperature and moisture in a Mediterranean riparian forest along a groundwater level

**24** gradient; (2) To determine soil moisture thresholds at which SR is rather controlled by

25    soil moisture than by temperature; (3) To compare SR responses under different tree

26    species present in a Mediterranean riparian forest (Alnus, glutinosa, Populus nigra and

27    Fraxinus excelsior). Results showed that the heterotrophic soil respiration rate,

28    groundwater level and 30 cm integral soil moisture ($SM_{30}$) decreased significantly from

29    riverside to uphill and showed a pronounced seasonality. SR rates showed significant

30    differences among tree species, with higher SR for P. nigra and lower SR for A.

31    glutinosa. The lower threshold of soil moisture was 20% and 17% for heterotrophic and

32    total SR respectively. Daily mean SR rate was positively correlated with soil

33    temperature when soil moisture exceeded the threshold, with $Q_{10}$ values ranging from

34    1.19 to 2.14; nevertheless, SR became decoupled from soil temperature when soil

35    moisture dropped below these thresholds.

36    **1    Introduction**

37    Soil is the largest pool of terrestrial organic carbon in the biosphere, storing around

38    2344 Pg C in the top 3 m (Jobbágy and Jackson, 2000). Soil respiration (SR) is the main

39    carbon efflux from ecosystems to the atmosphere, accounting for 60-90% of the total

40    ecosystem respiration (Schimel et al., 2001; Raich et al., 2002). Thus, SR plays an

41    important role in the global carbon balance (Schimel et al., 2001; Raich, Potter, &

42    Bhagawati, 2002), and even small changes of SR may induce positive feedbacks to

43    climate change (Schlesinger and Andrews, 2000). Therefore, information of how SR

44    interacts with environmental conditions, such as the response of specific components of

45    soil respiration to temperature and moisture changes, will be a key prospect for the

46    improvement of process-based models.

47    At the large scale, such as ecosystem and biome, net primary production (NPP) may be

48    the most important factor controlling SR (Wardle, 2002). NPP provides the inputs to the

49    soil from aboveground litter and also belowground organic detritus (Raich and Potter,

50  1995). Moreover, root respiration is strongly depended on the translocation of

51  photosynthates from the aboveground part of the plant (Curiel-Yuste et al., 2004). At

52  the smaller scale, SR has been found to be is very sensitive to soil temperature and soil

53  moisture (Fang & Moncrieff, 2001). Soil temperature has been recognized as the most

54  important environmental factor controlling SR because it affects the respiratory

55  enzymes of both roots and soil microbial biomass (Xu et al., 2011). In general, SR

56  increases exponentially with increases of soil temperature (Epron, Daniel et al., 1999;

57  Lloyd and Taylor, 1994; Mielnick and Dugas, 2000). In contrast to the positive

58  relationship between SR and soil temperature, both very high and very low soil

59  moisture has been shown to diminish the temperature response of SR (Londo et al.,

60  1999; Welsch and Hornberger, 2004) due to the potential oxygen limitations under high

61  soil moisture (Skopp et al., 1990) and due to metabolic drought stress under very low

62  soil moisture (Orchard and Cook, 1983). Soil moisture also affects the plant

63  composition and productivity (Häring et al., 2013) and thus, controls the quantity and

64  quality of both soil organic matter (SOM) and root exudate supply (Rustad et al., 2000).

65  Plenty studies have reported the effect of temperature or moisture on SR. However,

66  studies about the combined effects of both factors are relatively few and the information

67  of how soil moisture affects the relationship between soil temperature and SR is scarce

68  (Bowden et al., 1998; Davidson et al., 2006; Curiel-Yuste et al., 2007). In

69  Mediterranean and semiarid ecosystems, SR is highly sensitive to soil moisture and the

70  temperature-driven increases in SR are likely dampened by low soil moisture (Conant et

71  al., 2004; Raich and Potter, 1995; Rey et al., 2002). It is still unclear that under which

72  circumstance or environmental condition, the primary control factor of SR would switch

73  from temperature to soil moisture.

74    SR can be divided into autotrophic and heterotrophic respiration by different biological

75    sources (Hanson et al., 2000). Autotrophic respiration, also known as root respiration, is

76    mainly dependent on NPP, tree physiology such as photosynthesis substrate supply

77    (Heinemeyer et al., 2007; Hogberg et al., 2001). Heterotrophic respiration is the sum of

78    microbial decomposition of SOM (Fang et al., 2005; Knorr et al., 2005). In theory, due

79    to the different origins of autotrophic and heterotrophic respiration, they may have

80    different sensitivities toward environmental factors and respond differently to

81    seasonality (Epron et al., 2001; Kuzyakov and Larionova, 2006; Yan et al., 2010).

82    Riparian areas represent higher soil moisture and more sustained water tables (McGlynn

83    and Seibert, 2003). In these ecosystems, tree species composition and tree growth is

84    strongly influenced by the topographic position concomitant with the changes in the soil

85    water content. Thus, this may indirectly affect SR through litter input and nutrient

86    availability. Because of the retardation of microbial decomposition with the frequent

87    saturation of soil water, riparian areas tend to accumulate more SOM than hillslope

88    areas do (Sjögersten et al., 2006).

89    The main objectives of this study were: (1) to investigate the seasonal variations and

90    relationships between SR and both soil temperature and moisture in a Mediterranean

91    riparian forest along a groundwater level gradient; (2) To determine soil moisture

92    thresholds at which SR is rather controlled by soil moisture than by temperature, even in

93    such non-water stressed environments; (3) To compare SR responses under different

94    tree species present in a Mediterranean riparian forest (*Alnus glutinosa, Populus nigra*

95    and *Fraxinus excelsior*). With these aims, we carried out measurements of SR under

96    different tree species along a groundwater level gradient in a riparian forest in NE Spain.

97    The results of our study may help to better understand the interactions between different

98　components of SR with soil temperature and moisture, as well as the role of different

99　tree species. It also provides relevant information for SR model's parameterization.

100

101　## 2　Material and methods

102　### 2.1　Site description

103　The experiment was conducted in a riparian forest growing along Font de Regàs stream,

104　a headwater tributary of La Tordera river, in Montseny Natural Park (North of

105　Barcelona; 41º50'N, 2º30'E, altitudinal range 300-1200 m a.s.l.). The forest community

106　of our study site consists of black alder (*Alnus glutinosa* L.), black locust (*Robinia*

107　*pseudoacacia* L.), common ash (*Fraxinus excelsior* L.), and black poplar (*Populus*

108　*nigra* L.). As result of water and nutrient availability, *A. glutinosa* and *P. nigra* are

109　mostly distributed nearby the river whereas *F. excelsior* are located further away on the

110　upper site, near to the hill. *R. pseudoacacia* trees are scattered over the study area and

111　were not monitored. Mean annual temperature is 12ºC with maximum and minimum

112　average temperatures of 10 and 14ºC, respectively. The mean annual precipitation is

113　872 mm (1951-2010). The riparian soil is sandy-loam with low rock content (<13%),

114　weakly acidic (pH of 6.7), and has an average bulk density of 1.09 g/cm$^3$.

115　### 2.2　Experimental design

116　We divided the groundwater gradient (riparian-hillslope transect) into 4 levels according

117　to the distance from the riverside and tree species composition (Fig. 1). The distances of

118　level 1 to level 4 (L1 to L4) from the river centre were 2.7, 4.4, 6.8 and 11.8 m,

119　respectively. The three target tree species, *A. glutinosa, P. nigra* and *F. excelsior* were

120　located at level L1, L2 and L3, respectively. To examine the interaction effects on SR of

121　tree species, soil moisture and temperature, we set three transects crossing the

122 riparian-hill to measure the variation of total SR (sum of soil autotrophic and

123 heterotrophic respiration, hereafter referred to collectively as total SR, $SR_{tot}$) from

124 different tree species. Soil chambers were placed 1.5 m from the stem of the target tree

125 species. Moreover, we also set two transects to measure the topographic effects on soil

126 heterotrophic respiration ($SR_H$). Due to the difficulty of trenching next to the riverbank,

127 chambers for $SR_H$ were set only at level L2, L3 and L4. To separate root respiration

128 from $SR_H$, we inserted a PVC tube (diameter: 65cm, height: 40cm) into the soil five

129 months before starting the measurements. To avoid constraints on groundwater table

130 level fluctuations by the PVC tube, we cut two opposite windows on the PVC tube and

131 covered by 65 μm mesh to prevent root growth through the windows.

132 Stainless-steel rings were inserted permanently into the soil, down to 3 cm depth, as the

133 base of the soil chambers, and kept free from seedlings throughout the experiment

134 duration. The distances of each soil chamber from the riverside varied slightly due to

135 the tree distribution.

136 **2.3　Field measurement**

137 SR and soil temperatures were measured seasonally from summer 2011 to autumn 2012.

138 These measurements were conducted continuously for one week within each season. A

139 heavy rainfall event took place in winter 2012, resulting in elevated water levels of the

140 river that washed away most of the litter layer within three meters distance from the

141 river bank.

142 $CO_2$ concentration was measured in situ with an automatic changeover open system.

143 The system consists of an infrared gas analyzer (IRGA, LiCor 6262, LiCor, Inc.,

144 Lincoln, NE, USA), a datalogger (CR10, Campell Scientific Inc., UT, USA), 12 pairs of

145 channels, 12 soil chambers, 12 pairs of rotameters, 6 pumps and two flowmeters. Each

146  pair of channels consists of two tubes connected to a soil chamber, one attached on the

147  top of chamber (reference $CO_2$ concentration) and another attached at the base for

148  calculating the increment of $CO_2$ concentration provided by SR. Soil chambers were

149  placed from the beginning of each field campaign and $CO_2$ concentrations were

150  analysed and recorded sequentially over1-minute interval at each chamber. Air was

151  continuously forced through all chambers by pumps. Only one chamber at a time was

152  connected to the IRGA to analyse the $CO_2$ concentration of the respective chamber,

153  while air from the others was exhausted to the atmosphere until their own turn. The

154  sequence was programmed every four 4 cycles of differential IRGA measurements from

155  12 chambers, and an additional cycle of absolute IRGA measurement, which was then

156  used to calculate the actual absolute ambient air concentration of $CO_2$ in ppm. The $CO_2$

157  concentration of the ambient air was determined as the difference between the scrubbed

158  sample, which flows through soda lime and $Mg(ClO_4)_2$ and the ambient air sample.

159  Soil chambers were protected by placing a 50*50 cm green fine mesh on top to avoid

160  possible heating by direct sun light during the measurements. Soil temperature of 5 cm

161  depth was continuously measured with Pt100 temperature sensors and recorded in

162  parallel with the $CO_2$ concentration analysis. Thirty cm integral soil moisture ($cm^3/cm^3$,

163  $SM_{30}$) in each level were determined and recorded half-hourly with moisture

164  reflectometer (CS616, Campbell Scientific). Additionally, we also measured 5 cm

165  integral soil moisture ($SM_5$) next to each soil chamber once per day during each

166  measuring field campaign, with impedance probes (Delta-T Theta Probe Soil Moisture

167  Sensor, MI2x, Delta-T Devices, Cambridge, England). A grid of 28 wells (PVC tubes of

168  35mm in diameter) was installed to monitor groundwater table oscillation. Wells were

169  distributed along the study site and at different distances from the stream: 2.7, 4.4, 6.8,

170  11.8 m (n=7). Groundwater levels were monitored manually every two weeks using a

171  sounding device with acoustic and light signal (Eijelkamp, Agrisearch Euipment). In

172  autumn of 2012, after concluding the measurements, litter layer and soil samples (15 cm

173  depth) inside each chamber were collected. Litter layer samples were weighted after

174  oven-drying at 65-70ºC for 24h. Soil samples were first oven-drying at 105ºC and then

175  analyzed to determine their organic carbon and nitrogen content by using

176  Walkley-Black method and Kjeldahl method, respectively.

177  **2.4  Statistical analysis**

178  Statistical analyses were performed with PASW statistics 18 (SPSS Inc., 2009, Chicago,

179  IL). The missing data of soil temperatures were estimated from air temperature values

180  based on a regression analyses between air and soil temperatures. SR, soil temperature

181  and soil moisture data were analyzed using ANOVA to examine whether seasonal SR

182  rates were different among levels and tree species. Data used to test the significance in

183  ANOVA were based on daily means. Least significant difference (LSD) was used to

184  detect differences among levels and tree species for each season. We used regression

185  analysis to examine the relationship between SR and soil temperature. An univariate

186  exponential equation was fitted (van't Hoff, 1898)

187  $SR = ae^{bT}$                                          (1)

188  where SR is soil respiration rate ($\mu$mol C m$^{-2}$·s$^{-1}$), T is soil temperature (ºC), *a* is basal

189  respiration and b is the temperature sensitivity of SR. A $Q_{10}$ value for the whole

190  measurements period was computed for each topographic position and tree species on

191  the basis of daily average SR rate and soil temperature. In addition, we estimated

192  specific $Q_{10}$ values for summer of 2011 and 2012. Data collected were fitted to the

193  exponential equation. The apparent $Q_{10}$ was calculated as:

194  $Q_{10} = e^{10b}$                                          (2)

195  In order to understand the interaction between soil temperature and soil moisture and

196    the effect of soil moisture on regulating SR, we applied recursive partitioning analysis

197    to search for the threshold of soil moisture. As models based on partitioning can only

198    handle linear models, the equation above was transformed by linearizing with

199    logarithms:

200    $\ln SR = \ln a + bT$                                                                  (3)

201    Logarithmic transformed SR values were used as the dependent variable. Once the soil

202    moisture thresholds were obtained, linear and nonlinear regression analyses were used

203    to determine the relationship between SR, soil temperature and soil moisture in each

204    soil moisture interval. The recursive partitioning analysis was conducted in the R

205    statistical environmental using the *party* package (Zeileis et al., 2008).

206

207    **3    Results**

208    **3.1    Seasonal variation of groundwater level, soil moisture and soil**

209             **temperature**

210    Seasonal variation of air temperature and precipitation was remarkable. The

211    precipitation in 2011 was significantly higher than in 2012, especially in summer.

212    Summer precipitation in 2011 was four times higher (183 mm) than in 2012 (39 mm).

213    $SM_{30}$ was significantly higher at L1 (Fig. 2). In summer 2012, due to a remarkable

214    drought, $SM_{30}$ at L1 only showed a small decrease with respect to summer 2011; while

215    at the other levels (L2, L3 and L4) $SM_{30}$ was markedly decreased. Groundwater levels

216    showed no seasonal variation but were significantly different among them.

217    Soil nearby the river contained less organic carbon and nitrogen, but a higher C:N ratio,

218    with a C:N ratio of 12.13 (Tab. 1). Soil C:N ratio decreased from the riverside to uphill

219    whereas the dry weight of litter layer increased from the riverside to uphill. The largest

220 amount of dry weight of litter layer was found under *F. excelsior*, and coincided with

221 the highest soil organic carbon (SOC) and soil nitrogen concentration among levels.

222

## 3.2 Seasonal variation of $SR_H$ along hillslope transect

224 $SR_H$ rates ranged from 0.17μmol C $m^{-2}s^{-1}$ (in winter, L4) to 1.69μmol C $m^{-2}s^{-1}$ (in

225 summer, L2, Fig. 3). $SR_H$ decreased significantly from riparian zone (L2) to hill zone

226 (L4), especially in summer. $SR_H$ measured from different levels were significantly

227 different in all seasons (P<0.05). $SR_H$ at L2 had a higher variability during the whole

228 experiment. Minimum soil temperature coincided with maximum $SM_5$ in winter while

229 maximum soil temperature was recorded in summer when $SM_5$ was lowest. $SR_H$ varied

230 markedly during the year following the change of soil temperature from summer 2011

231 to spring 2012, and the changes of $SM_5$ for summer and autumn 2012. As expected, $SR_H$

232 was lower during winter when soil temperatures were the lowest of the year, and $SR_H$

233 was higher during the growing season. $SM_{30}$ at L2 was significantly lower than $SM_{30}$ at

234 L1, but higher than $SM_{30}$ at L3 and L4.

235

## 3.3 Tree species effects on $SR_{tot}$

237 The observed variation of $SR_{tot}$ for the three tree species followed the change of soil

238 temperature over the year (Fig. 3). $SR_{tot}$ of *P. nigra* was the highest one, especially

239 during summer, and $SR_{tot}$ of *A. glutinosa* was the lowest one throughout the year. There

240 were no significant differences of soil temperatures among tree species locations. $SM_5$

241 did not differ among tree species location but there was a tendency towards a higher

242 $SM_5$ under *F. excelsior*. $SM_{30}$ was significantly different among levels for all seasons.

243 The variation of $SM_{30}$ at L1 was lower and showed less seasonal variability, maintaining

244 most of the $SM_{30}$ values around 40%. During both summers 2011 and 2012, $SM_{30}$ at L3

245 dropped untill around 10%, which is even lower than the $SM_5$ at L4 where *F. excelsior*

246 is found.

## 3.4 Drought and rain pulse effects on SR

248 The precipitation of 39 mm of summer 2012 was 21% lower than precipitation of

249 summer 2011. This lower precipitation caused a significant reduction of around 50% of

250 $SM_5$, 14-35% of $SM_{30}$ and at the same time a reduction of SR between 21 and 49%. The

251 $Q_{10}$ values ranged from 0.97 to 1.40 in summer 2011 and 0.63 to 1.14 in summer 2012

252 (Tab. 2).

253 A rainfall event (13 mm) during the measurement period of summer 2012 caused a

254 significant increase of soil moisture and SR rates at all levels (L1 to L4). The $SM_5$

255 increased around 21-74% after the rainfall event even though it only caused a 0-20%

256 increase of the $SM_{30}$ (Tab. 3). This rainfall event caused a sharp increase of SR from

257 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

258 of SR around 34 to 68%.

259

## 3.5 The switch of primary control factor of SR

261 We identified three $SM_5$ intervals for each $SR_H$ and $SR_{tot}$ (Tab. 4), which suggest the

262 existence of thresholds in soil moisture effect. SR was positively related (P<0.001) to

263 soil temperature when soil moisture was higher than 23% for $SR_H$, or higher than 27%

264 for $SR_{tot}$. The lower threshold for $SR_H$ and $SR_{tot}$ were 20% and 17% of $SM_5$ respectively.

265 Under the low bound value, $SR_H$ showed a significantly positive relation with $SM_5$ (Fig.

266 4, linear regression with $r^2$ of 0.89, 0.92 and 0.91 for L2, L3 and L4) while $SR_{tot}$ showed

267 a weak positive relation with $SM_5$ (Fig. 5, linear regression with $r^2$ of 0.56, 0.11 and

268    0.10 for L1, L2 and L3). The exponential model based on soil temperature accounts for

269    68% to 84% of the variation in both $SR_H$ and $SR_{tot}$ rates at the higher $SM_5$ interval

270    values. The fitted $Q_{10}$ values in high $SM_5$ interval ranged from 1.49 to 2.14. Generally

271    the $Q_{10}$ values of $SR_H$ were lower than the $Q_{10}$ of $SR_{tot}$.

272

273    **4    Discussion**

274    **4.1    Effect of groundwater level and soil moisture on SR**

275    In studies of Martin and Bolstad (2005) and Pacific et al. (2008), it was indicated that

276    the amount and availability of soil water varies depending on landscape position and

277    topography. Both studies also show that small differences in micro-topography appear

278    to be important in driving soil moisture conditions. This is in accordance with our

279    results; the overall seasonal trends of soil moisture were similar, but differences in the

280    relative magnitude of soil moisture still can be found among levels.

281    In our study site, the $SR_H$ was significantly higher at L2 and decreased with the distance

282    from the river. At the same time, $SR_{tot}$ of *A. glutinosa* at L1 was significantly lower than

283    the other two species found at L2 and L3. This result could be explained by limitations

284    to SR imposed by groundwater level in two different ways. First, when groundwater

285    level is low, drought stresses soil microbial and root respiration activity, and secondly

286    when groundwater level is high and close to topsoil surface, it limits soil aeration and

287    likely reduces the effective respiring soil volume. Pacific et al. (2008) showed that the

288    soil $CO_2$ concentrations were significantly higher in the riparian zone as a result of

289    higher soil moisture. In contrast, Zanchi et al. (2011) found lower SR in plots after

290    drainage, and suggested that the low C and N content in the topsoil near to the river,

291    where most of the soil $CO_2$ respiration is produced, could partially explain that low SR.

292     The discrepancy of these two studies could be associated to the different drainage

293     regimes, as the poorly drained plots imply an anaerobic inhibition of SR. In our study,

294     however, $SR_H$ was measured at L2, L3 and L4 under well-drained conditions and $SR_H$

295     decreased concomitantly with the decrease in the availability of soil water. Nonetheless,

296     $SR_{tot}$ of *A. glutinosa* was measured at L1, where the soils sometimes experienced

297     flooding or not well-drained conditions, and the root respiration may be inhibited by the

298     high groundwater level.

299     Additionally, landscape position and topography not only altered the availability of soil

300     water but also affected the annual range of soil moisture. This is shown by Zanchi et al.

301     (2011) studying riparian SR in Amazonia. They indicate that riparian soil is very

302     sensitive to the changes of water flooding regime. The high groundwater table in

303     riparian zones implies intermittent anaerobic conditions and the inhibition of diffusion

304     during water saturation. These differences in soil moisture caused by site topography

305     may result in differences in SR even though the soil temperatures were similar among

306     sites. The different behaviours of $SR_H$ and $SR_{tot}$ from L1 to L4 from our results indicate

307     a different contribution of $SR_H$ to $SR_{tot}$. As the root system of *A. glutinosa* may

308     constantly experience a saturated water regime, the relative contribution from root

309     respiration may be much lower than the one of the other two species.

310     **4.2   Rain pulse and drought effects on SR**

311     The Mediterranean climate is characterized by summer droughts that affect particularly

312     the top soil layers, therefore rainfall events during these dry periods can trigger abrupt

313     increases in SR for days (Bowling et al., 2011; Cisneros-Dozal et al., 2007; Lee et al.,

314     2004; Unger et al., 2010). Lee et al. (2004) simulated precipitation and found that

315     hardwood forest floors were very sensitive to changes in moisture in the upper soil

316     layers. Moreover, Wang et al. (2012) noted that the response of litterfall respiration is

317 very sensitive to rainfall, and the increase in soil moisture by rainfall primarily

318 enhanced the litterfall respiration but depressed mineral SR. Similar results were

319 published by Casals et al. (2011) reporting that SR after a precipitation pulse was mostly

320 derived from $SR_H$ with a contribution up to 70% of $SR_{tot}$. Hence, our findings seem to

321 be consistent with these previous studies.

322

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

324 This study aimed at assessing the importance of soil moisture on soil respiration and

325 determining the threshold of soil moisture at which soil moisture overrules temperature

326 in controlling SR. The response of SR to soil moisture has been widely studied and

327 described by various types of functions, such as linear or logarithmic functions

328 depending on the soil type, climate or vegetation type (Comstedt et al., 2010; Epron,

329 Daniel et al., 1999; Orchard and Cook, 1983). In our study, the seasonal courses of $SR_H$

330 and $SR_{tot}$ generally followed the seasonal cycle of temperature, but moderated by soil

331 moisture. Such a relationship is in agreement with other previous studies (Davidson et

332 al., 1998; Martin and Bolstad, 2005; Wang et al., 2013).

333 The positive linear relationship between SR and soil moisture in low soil moisture

334 conditions found in our work agrees with many previous studies where low soil

335 moisture constrains SR (Almagro et al., 2009; Davidson et al., 1998; Keith et al., 1997;

336 Rey et al., 2002; Wang et al., 2013; Xu and Qi, 2001). In our study, the low soil

337 moisture and   warmer temperatures actually reduced SR rates, resulting in lower $Q_{10}$

338 values at the lower soil moisture . A similar decline of $Q_{10}$ with decreasing soil moisture

339 has been reported by Conant et al.(2004), Curiel Yuste et al. (2003) and Wen et al.

340 (2006). Low soil water content not only reduces the contact between substrate and

341 enzymes and microbes, it also decreases the substrate supply due to the increased

342    drying-out of litter and topsoil layer (Davidson et al., 2006). Another possible reason for

343    the observed lower $Q_{10}$ is that the reduction of photosynthesis decreases the

344    translocation of photosynthates to the rhizophere (Hogberg et al., 2001; Nordgren et al.,

345    2003).

346    In a Norway spruce stand, Gärdenäs (2000) found that litter moisture explained most of

347    the variation of SR whereas mineral soil moisture, air or litter temperatures were not

348    significantly affected. Our results showed that the seasonal variations of $SR_H$ and $SR_{tot}$

349    were mainly controlled by soil temperature, with secondary influence by soil moisture

350    ($SM_5$). Using the recursive partitioning method, we have identified clear thresholds for

351    $SM_5$ effects on the temperature sensitivity of SR. Soil moisture thresholds at which SR

352    temperature sensitivity is reduced have been found in several studies, from different

353    ecosystems (Fang and Moncrieff, 2001; Gaumont-Guay et al., 2006; Jassal et al., 2008;

354    Lellei-Kovács et al., 2011; Palmroth et al., 2005; Wang et al., 2013). However, the

355    threshold values in soil moisture seem to be site specific, as the factors limiting water

356    uptake by plants and microbes may differ among ecosystems. Even in the same climate

357    region, different soil moisture thresholds have been found from previous studies. For

358    example, Almagro et al. (2009) investigated how soil moisture modulated the sensitivity

359    of soil respiration in different ecosystems in the Mediterranean region and found that

360    the threshold value of soil moisture was 10%. Above this soil moisture values, $Q_{10}$

361    ranged from 1.86 to 2.20 and decreased to 0.44 to 0.63 when soil moisture was lower

362    than 10%. Furthermore, Rey et al. (2002) found in a Mediterranean oak forest that soil

363    temperature accounted for 85% of the variation of SR when soil moisture was above

364    20% with a $Q_{10}$ value of 2.34. Nonetheless, Xu and Qi (2001) found that with soil

365    moisture higher than 14%, the $Q_{10}$ value was 1.8 and decreased to 1.4 when soil

366    moisture was lower than 14%.

367

### 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

393 environment such as riparian forests. Our findings provide support for modelling

394 approaches that include soil temperature and soil moisture, by making available

395 parameters to predict SR rates. This study has also implications for a better

396 understanding of global change impacts on the carbon cycle, since soil water

397 availability will likely become an increasingly crucial factor for some regions that are

398 expected to suffer more frequent and severe droughts 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.

| Groundwater level | C/N | SOC % | NITROGEN% | Litter Layer (kg/m$^2$) |
|---|---|---|---|---|
| L2- Near river | 10.40 | 2.73 | 0.16 | 0.97 |
| L3- Intermediate | 10.00 | 4.38 | 0.26 | 1.20 |
| L4- Uphill | 9.15 | 3.36 | 0.23 | 1.67 |
| L1- *A. glutinosa* | 12.13 | 2.29 | 0.11 | 0.69 |
| L2- *P. nigra* | 10.27 | 3.52 | 0.20 | 1.18 |
| L3- *F. excelsior* | 9.67 | 4.85 | 0.30 | 2.21 |

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Table 2. Comparison of soil respiration rates (SR), soil moistures (SM) and Q10 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 ($SM_{30}$).

| | Chamber | SR ($\mu mol\ C\ m^{-2}s^{-1}$) | | | $SM_5$(%) | | | $SM_{30}$(%) | | | Q10 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2011 | 2012 | Reduction | 2011 | 2012 | Reduction | 2011 | 2012 | Reduction | 2011 | 2012 |
| $SR_H$ | L2- Near river | 1.65 | 0.84 | 49% | 27.10 | 14.94 | 45% | 22.22 | 14.51 | 35% | 1.09 | 0.76 |
| | L3- Intermediate | 0.98 | 0.70 | 28% | 31.68 | 14.91 | 53% | 12.60 | 9.22 | 27% | 1.04 | 0.88 |
| | L4- Uphill | 0.74 | 0.50 | 32% | 38.02 | 14.19 | 63% | 10.87 | 8.13 | 25% | 0.97 | 0.84 |
| $SR_{tot}$ | L1- *A. glutinosa* | 1.24 | 0.78 | 37% | 27.24 | 13.04 | 52% | 42.49 | 36.58 | 14% | 1.31 | 0.80 |
| | L2- *P. nigra* | 1.42 | 1.13 | 21% | 26.22 | 12.93 | 51% | 22.22 | 14.51 | 35% | 1.17 | 0.63 |
| | L3- *F. excelsior* | 1.26 | 0.76 | 40% | 26.45 | 12.87 | 51% | 12.60 | 9.22 | 27% | 1.40 | 1.14 |

593     *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 ($SR_H$). Total SR ($SR_{tot}$). Five cm integral soil moisture ($SM_5$). Thirty cm integral soil moisture ($SM_{30}$). Data were averaged for two days before and two days after the rainfall event

| | Chamber | SR($\mu$mol C m$^{-2}$s$^{-1}$) | | | $SM_5$ (%) | | | $SM_{30}$ (%) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | before | after | increase | before | after | increase | before | after | Increase |
| $SR_H$ | L2- Near river | 0.66 | 1.00 | 52% | 14.09 | 18.84 | 34% | 14.45 | 14.50 | 0% |
| | L3- Intermediate | 0.59 | 0.80 | 34% | 15.19 | 18.37 | 21% | 8.46 | 10.15 | 20% |
| | L4- Uphill | 0.41 | 0.59 | 45% | 12.06 | 17.51 | 45% | 6.97 | 9.64 | 38% |
| $SR_{tot}$ | L1- *A. glutinosa* | 0.67 | 1.04 | 54% | 11.27 | 16.91 | 50% | 36.13 | 37.48 | 4% |
| | L2- *P. nigra* | 0.99 | 1.66 | 68% | 10.86 | 18.86 | 74% | 14.45 | 14.50 | 0% |
| | L3- *F. excelsior* | 0.68 | 0.98 | 44% | 11.10 | 17.20 | 55% | 8.46 | 10.15 | 20% |

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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 5cm integral soil moisture.

| | | $SM_5 > 23\%$ | | | $23\% > SM_5 > 20\%$ | | | $SM_5 < 20\%$ | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Fn | $R^2$ | Q10 | Fn | $R^2$ | Q10 | Fn | $R^2$ | Q10 |
| $SR_H$ | L2- Near river | $SR_H=0.52e^{0.05T}$ | $0.77^{***}$ | 1.58 | $SR_H=0.68e^{0.02T}$ | $0.74^{*}$ | 1.25 | $SR_H=2.10.e^{-0.4T}$ | $0.58^{**}$ | 0.02 |
| | L3- Intermediate | $SR_H=0.51e^{0.04T}$ | $0.72^{***}$ | 1.49 | $SR_H=0.67e^{0.05T}$ | $0.70^{*}$ | 1.65 | $SR_H=2.11e^{-0.04T}$ | $0.57^{**}$ | 0.66 |
| | L4- Uphill | $SR_H=0.40e^{0.05T}$ | $0.84^{***}$ | 1.58 | $SR_H=0.64e^{0.02T}$ | $0.66^{*}$ | 1.19 | $SR_H=1.34e^{-0.03T}$ | $0.34^{*}$ | 0.76 |
| | | $SM_5 > 27\%$ | | | $27\% > SM_5 > 17\%$ | | | $SM_5 < 17\%$ | | |
| $SR_{tot}$ | L1- *A. glutinosa* | $SR_{tot}=0.53e^{0.04T}$ | $0.77^{***}$ | 1.54 | $SR_{tot}=0.69e^{0.03T}$ | $0.83^{***}$ | 1.30 | $SR_{tot}=0.77e^{0.01T}$ | 0.01 | 1.06 |
| | L2- *P. nigra* | $SR_{tot}=0.52e^{0.05T}$ | $0.78^{***}$ | 1.60 | $SR_{tot}=0.61e^{0.04T}$ | $0.80^{***}$ | 1.46 | $SR_{tot}=1.39e^{-0.02T}$ | $0.19^{**}$ | 1.17 |
| | L3- *F. excelsior* | $SR_{tot}=0.32e^{0.08T}$ | $0.68^{***}$ | 2.14 | $SR_{tot}=0.56e^{0.03T}$ | $0.62^{***}$ | 1.40 | $SR_{tot}=1.30e^{-0.02T}$ | $0.25^{**}$ | 0.82 |

597     *** P<0.001 ;    ** P<0.01 ; * P<0.05

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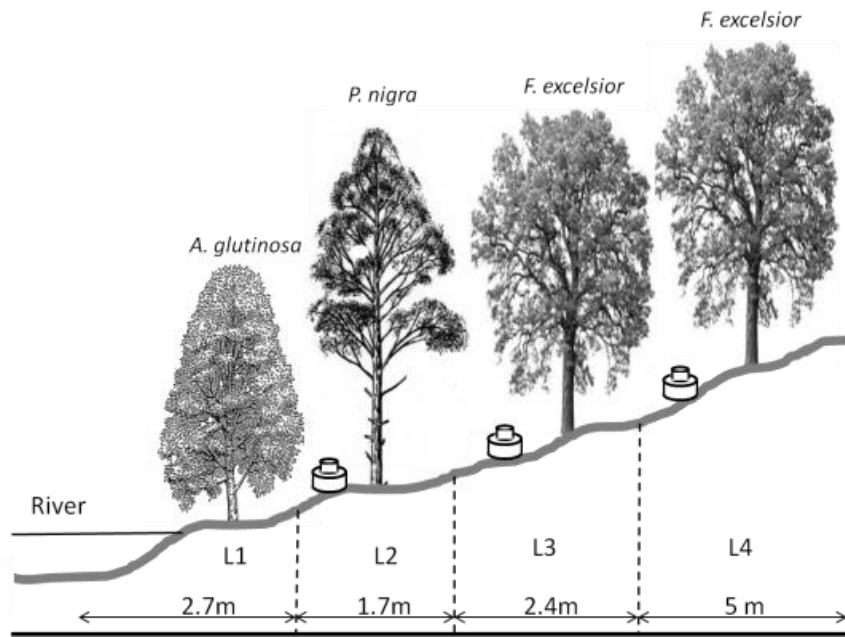


600 Fig. 1. Sketch of levels in a gradient of soil water availability with tree species
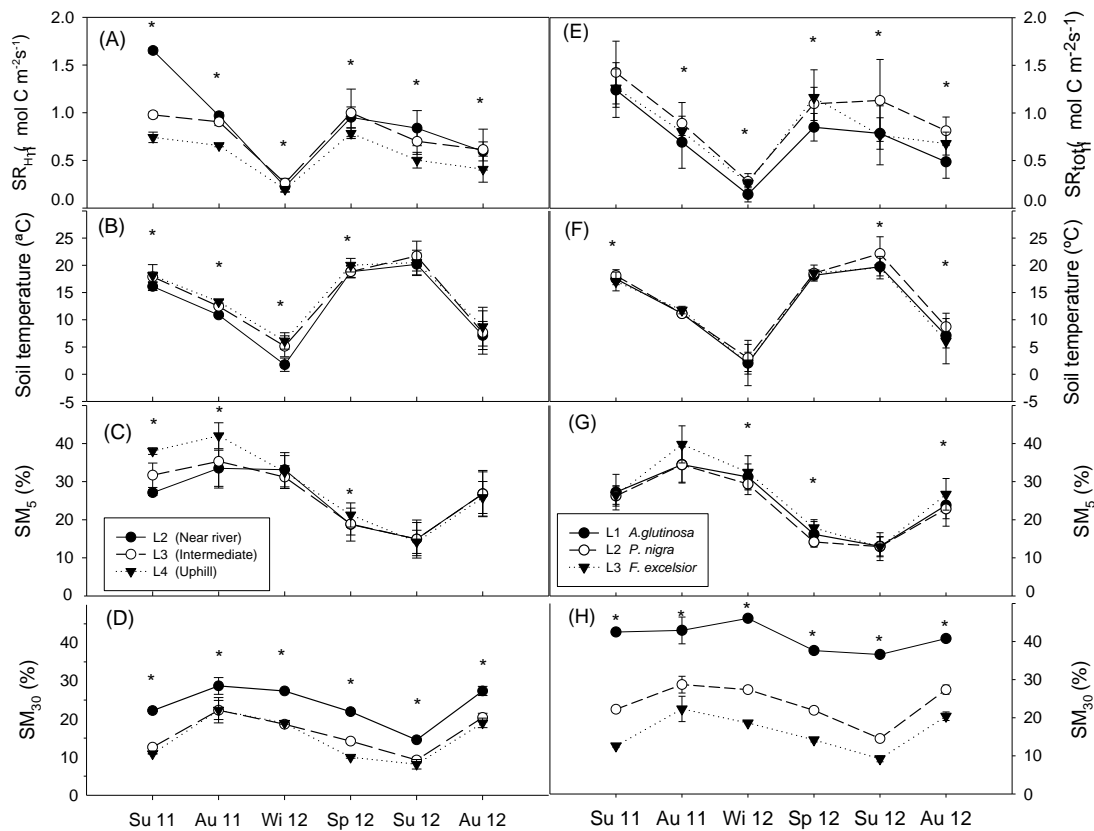601 distribution and $SR_H$ chamber positions.

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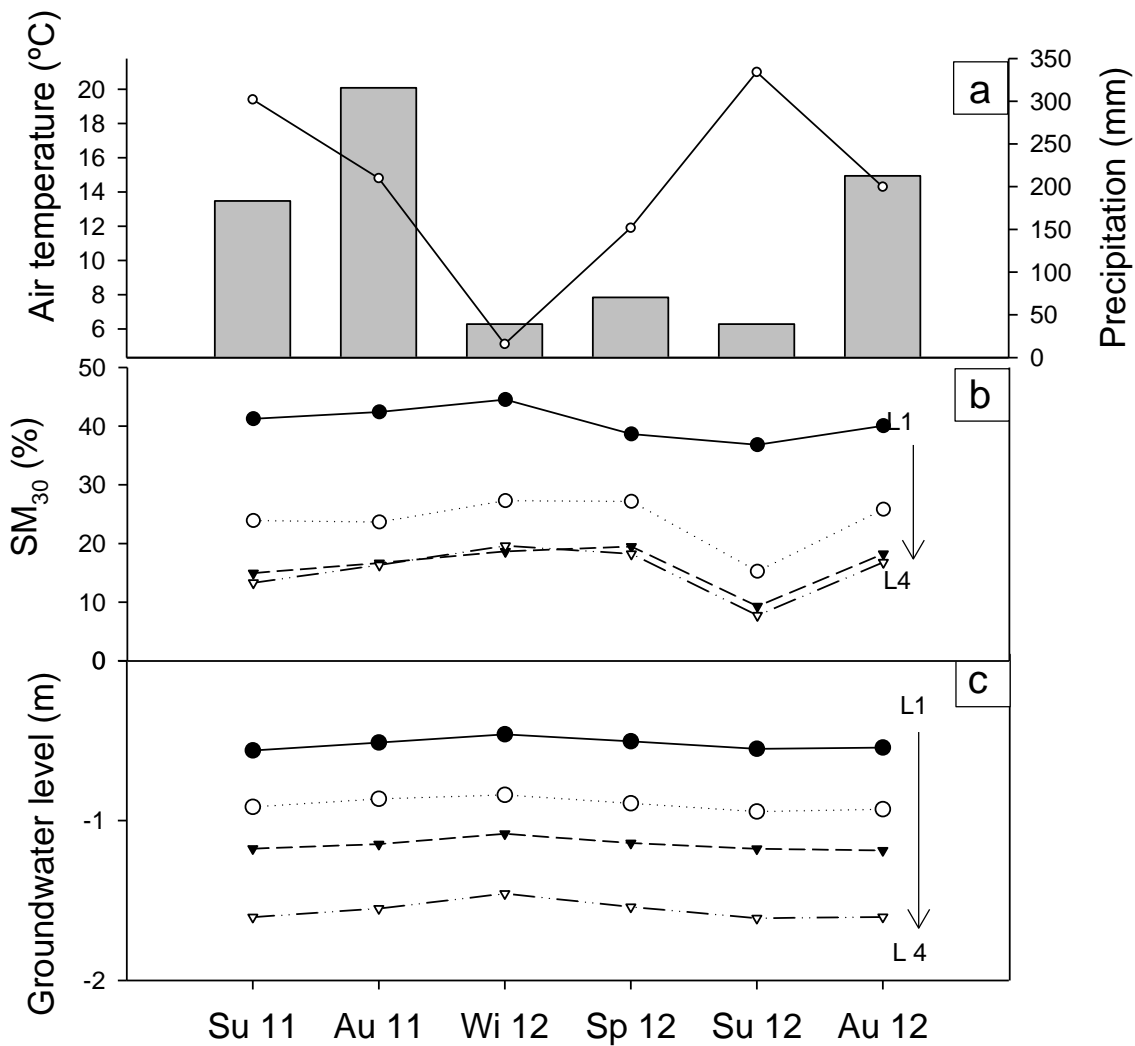
Fig 2. Seasonal changes of summer 2011 (Su11), autumn 2011 (Au11), winter 2012 (Wi 12), spring 2012 (Sp12) and autumn 2012 (Au12) in **a.** mean seasonal air temperature and precipitation; **b**. 30 cm integral soil moisture ($SM_{30}$); **c**. groundwater level, value represents the depth of groundwater level from soil surface (L1, L2, L3 and L4).

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Fig.3: Seasonal changes of summer 2011 (Su11), autumn 2011 (Au11), winter 2012 (Wi 12), 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 $P \leq 0.05$ (Detail please refer to Annex A & B).
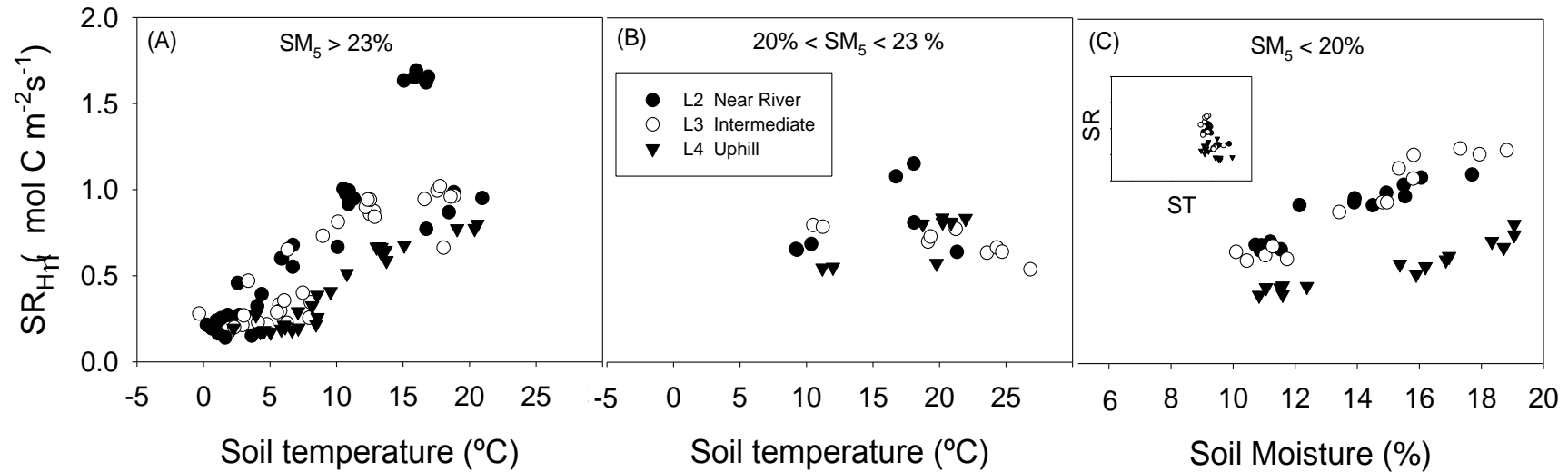
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Fig.4: Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factor for $SR_H$. (A) At $SM_5 \geq 23\%$, positive correlations of $SR_H$ with soil temperature in all levels. (B) At $20\% \leq SM_5 < 23\%$, transition 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)
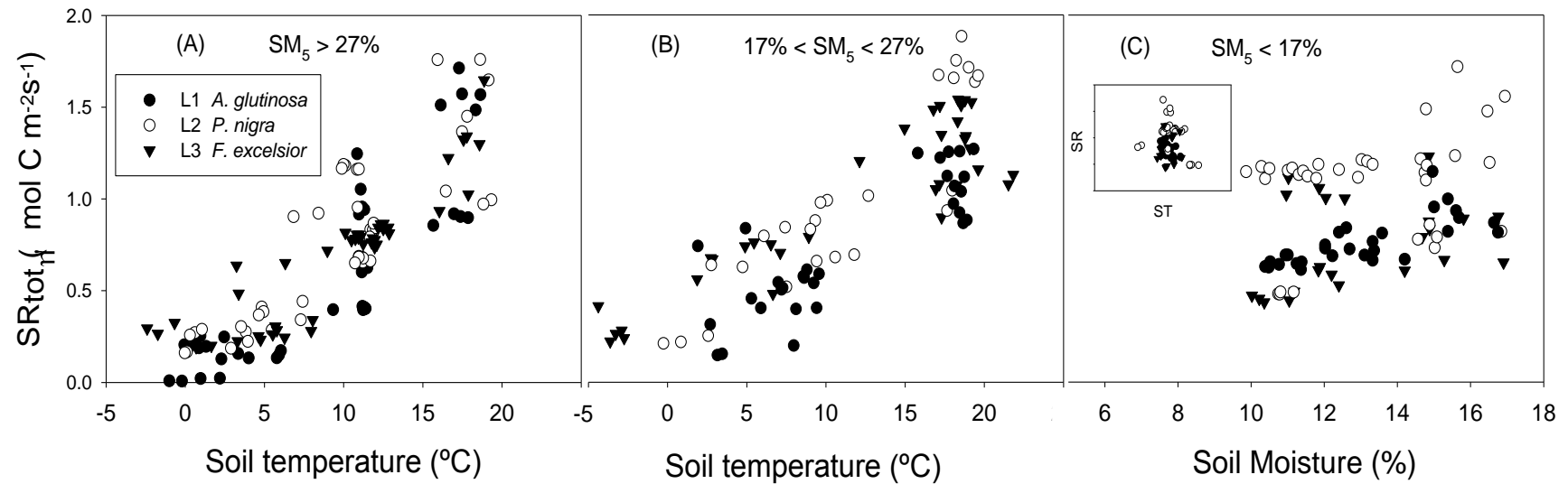
Fig.5: Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factor for $SR_{tot}$. (A) At $SM_5 \geq 27\%$, positive correlations of $SR_{tot}$ with soil temperature under all tree species. (B) At $17\% \leq SM_5 < 27\%$, positive but slightly weaker correlations of $SR_{tot}$ 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 $SR_{tot}$ 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)

Annex A. 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).

| Champaign | ST | | | $SM_5$ | | | $SM_{30}$ | | | $SR_H$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L2 | L3 | L4 | L2 | L3 | L4 | L2 | L3 | L4 | L2 | L3 | L4 |
| 2011 Summer | 16.11±0.73(A) | 17.88±0.88(AB) | 18.12±2.02(B) | 27.11±0.74(A) | 31.68±3.20(B) | 38.02±0.87(C) | 22.22±0.23(A) | 12.60±0.36(B) | 10.87±0.1(C)0 | 1.65±0.03(A) | 0.98±0.03(B) | 0.52±0.32(C) |
| 2011 Autumn | 10.87±0.30(A) | 12.48±0.24(B) | 13.33±0.25(C) | 33.51±4.75(A) | 35.33±7.00(A) | 42.05±3.40(B) | 28.69±2.20(A) | 22.31±3.32(B) | 22.37±2.51(B) | 0.97±0.04(A) | 0.90±0.04(B) | 0.66±0.01(C) |
| 2012 Winter | 1.75±1.22(A) | 5.13±1.92(B) | 6.11±1.50(B) | 33.14±4.50(A) | 31.21±3.00(A) | 32.52±4.30(A) | 27.35±0.22(A) | 18.61±0.18(B) | 18.90±0.24(C) | 0.22±0.66(AB) | 0.26±0.05(A) | 0.20±0.03(B) |
| 2012 Spring | 18.82±1.13(A) | 18.81±1.04(A) | 20.03±1.25(B) | 18.73±4.31(A) | 18.87±2.89(A) | 21.26±3.18(A) | 21.91±0.41(A) | 14.17±0.51(B) | 9.96±0.25(C) | 0.95±0.11(A) | 1.00±0.25(A) | 0.78±0.05(B) |
| 2012 Summer | 20.18±2.05(A) | 21.70±2.74(A) | 20.80±2.40(A) | 14.94±4.99(A) | 14.91±4.35(A) | 14.19±3.04(A) | 14.51±0.07(A) | 9.22±0.78(B) | 8.14±1.25(C) | 0.84±0.18(A) | 0.70±0.14(B) | 0.50±0.08(C) |
| 2012 Autumn | 7.11±2.58(A) | 7.66±3.98(A) | 8.73±3.38(A) | 26.87±6.08(A) | 26.77±5.80(A) | 25.84±4.21(A) | 27.27±1.12(A) | 20.38±1.03(B) | 19.01±1.14(C) | 0.59±0.10(A) | 0.61±0.21(A) | 0.41±0.14(B) |

Annex B. Analysis of variance (ANOVA) statistics for soil temperature (ST), soil moisture (SM):$SM_5$, $SM_{30}$, and total soil respiraion ($SR_{tot}$) of different tree species of the same season. LSD was used to test post hoc.

Means with the same letter are not significantly different ($P < 0.05$).

| Champaign | ST | | | SM$_5$ | | | SM$_{30}$ | | | SR$_{tot}$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *A. glutinosa* | *P. nigra* | *F. excelsior* | *A. glutinosa* | *P. nigra* | *F. excelsior* | L1 | L2 | L3 | *A. glutinosa* | *P. nigra* | *F. excelsior* |
| 2011 Summer | **17.51±1.07(AB)** | **18.11±1.09(A)** | **17.04±1.73(B)** | 27.24±4.67(A) | 26.22±2.65(A) | 26.45±2.42(A) | **42.49±0.45(A)** | **22.22±0.23(B)** | **12.60±0.36(C)** | 1.24±0.28(A) | 1.42±0.33(A) | 1.26±0.20(A) |
| 2011 Autumn | 11.16±0.20(A) | 11.11±0.71(A) | **11.77±0.69(B)** | 34.46±4.60(A) | 34.42±4.79(A) | 39.78±4.86(B) | **42.92±3.52(A)** | **28.69±2.20(B)** | **22.31±3.32(C)** | **0.69±0.27(AB)** | **0.89±0.22(B)** | **0.80±0.04(A)** |
| 2012 Winter | 2.02±2.00(A) | 3.00±2.49(A) | 2.05±4.17(A) | **31.24±3.42(AB)** | **29.36±2.76(A)** | **32.46±4.37(B)** | **46.08±0.11(A)** | **27.35±0.22(B)** | **18.61±0.18(C)** | 1.44±0.08(A) | 0.28±0.08(A) | **0.26±0.04(B)** |
| 2012 Spring | 18.16±0.84(A) | 18.53±0.64(A) | 18.57±1.48(A) | **16.19±2.80(A)** | **14.15±1.26(B)** | **17.86±2.16(A)** | **37.62±0.10(A)** | **21.91±0.41(B)** | **14.17±0.51(C)** | 0.85±0.14(A) | 1.10±0.17(A) | **1.16±0.29(B)** |
| 2012 Summer | **19.74±1.69(A)** | **22.15±3.11(B)** | **19.57±2.07(A)** | 13.04±2.55(A) | 12.93±3.65(A) | 12.87±2.60(A) | **36.58±0.63(A)** | **14.51±0.07(B)** | **9.22±0.78(C)** | 0.78±0.17(A) | 1.13±0.43(B) | 0.76±0.31(A) |
| 2012 Autumn | **7.08±2.27(AB)** | **8.71±2.49(A)** | **6.07±4.15(B)** | **23.80±3.53(A)** | **22.83±4.52(A)** | **26.66±4.15(B)** | **40.76±0.50(A)** | **27.27±1.12(B)** | **20.38±1.03(C)** | **0.49±0.17(A)** | **0.81±0.14(B)** | **0.68±0.12(C)** |