Universiteit Antwerpen

This item is the archived peer-reviewed author-version of:

Zea mays rhizosphere respiration, but not soil organic matter decomposition was stable across a temperature gradient

Reference:

Vicca Sara, Janssens Ivan, Wong Suan-Chin, Cernusak Lucas A., Farquhar Graham D..- **Zea mays** rhizosphere respiration, but not soil organic matter decomposition was stable across a temperature gradient
Soil biology and biochemistry - ISSN 0038-0717 - 42:11(2010), p. 2030-2033
Full text (Publishers DOI): http://dx.doi.org/doi:10.1016/j.soilbio.2010.07.023
Handle: http://hdl.handle.net/10067/841140151162165141

uantwerpen.be

Institutional repository IRUA

Short communication:

Zea mays rhizosphere respiration, but not soil organic matter decomposition was stable across a temperature gradient

Sara Vicca[1], Ivan A. Janssens[1,2], Suan-Chin Wong[2], Lucas A. Cernusak[2,3], Graham D. Farquhar[2]

[1] Universiteit Antwerpen, Universiteitsplein 1, B-2610 Wilrijk, Belgium

[2] Environmental Biology Group, Research School of Biology Australian National University, GPO Box 475, Canberra, ACT 2601, Australia

[3] School of Environmental and Life Sciences, Charles Darwin University, Darwin, NT 0909, Australia

Corresponding author: Sara Vicca

Email: Sara.Vicca@ua.ac.be

Tel.: +32 3 265 22 82

Fax: +32 3 265 22 71

Number of text pages: 12

Number of tables: 2

Number of figures: 2

Abstract

In a greenhouse experiment, we grew maize plants at different densities. We added fertilizer to half of the pots and created a temperature gradient. After 10 weeks of plant growth, we measured soil CO_2 efflux (SCE) and determined rhizosphere respiration (R_{rhizo}) and the decomposition rate of soil organic matter (R_{SOM}) using the different $\delta^{13}C$ of the C_3 soil and C_4 plants. Whereas R_{rhizo} remained stable across the temperature gradient, R_{SOM} significantly increased with growth temperature. Neither plant density, nor the fertilizer treatment affected the relation between R_{rhizo} or R_{SOM} and growth temperature. Although R_{rhizo} might still increase with temperature in the short term, long term exposure to higher temperatures revealed full thermal acclimation of R_{rhizo}, but not of R_{SOM}.

Keywords: Soil CO_2 efflux; Rhizosphere respiration; Soil organic matter decomposition; Stable carbon isotopes; Temperature gradient; Thermal acclimation

It was previously suggested that rhizosphere respiration (R_{rhizo}) and soil organic matter decomposition (R_{SOM}) respond differently to temperature (Boone *et al.* 1998; Hartley *et al.* 2007a; Moyano *et al.* 2007). Boone et al. (1998) found a higher temperature sensitivity of R_{rhizo} as compared to R_{SOM}, but this temperature response of R_{rhizo} was strongly affected by seasonal variations in plant phenology and photosynthetic substrate supply. Other studies suggested lower temperature sensitivity for R_{rhizo} than for R_{SOM} (Bhupinderpal-Singh *et al.* 2003; Hartley *et al.* 2007a; Moyano *et al.* 2007), whereas Bååth & Wallander (2003) and Schindlbacher et al. (2009) found similar temperature effects on R_{SOM} and R_{rhizo}. More research is obviously needed to verify that models need to apply different temperature responses for R_{SOM} and R_{rhizo}. In particular, the confounding effects of seasonal variations in, e.g., root growth should be excluded, as they can substantially alter apparent temperature responses (Curiel Yuste *et al.* 2004; Davidson *et al.* 2006). Also studies using trenching or girdling as partitioning method face important shortcomings, decreasing the reliability of their results (Kuzyakov 2006). In the current study, we avoided seasonal variations and used the ^{13}C natural abundance technique (growing C_4 plants in a soil with C_3 plant-derived organic matter) to determine effects of growth temperature on R_{rhizo} and R_{SOM}. In addition, we tested for effects of plant density and fertilizer addition.

We grew *Zea mays* in 40 pots (20 l) containing a homogenized soil mixture (20% silt, 80% sand; 5% organic matter was added as plant-derived compost; bulk density was 1.3 g cm^{-3}). To obtain a gradient in root mass and activity, which would be detectable in R_{rhizo}, we planted one, three, or six plants per pot. Furthermore, two nutrient treatments were created by adding 12 g slow-release fertilizer (Osmocote; N/P/K/Mg: 15/4.8/10.8/1.2; trace elements: B, Cu, Fe, Mn, Mo, Zn; Scotts Australia Pty Ltd) to half of the pots. All pots were irrigated roughly every 48 hours (water was added until it leached out at the bottom) and always in the evening prior to a

58 measurement campaign. We placed all pots randomly in a greenhouse, where plants were grown
59 at roughly 25 ˚C during daytime and 15 ˚C during night time. Because the experiment was
60 conducted in winter with cooler ambient temperatures, the greenhouse was permanently heated.
61 The heater was located at one end of the greenhouse, thus creating a temperature gradient with
62 soil temperatures in the afternoon around 28 ˚C near the heater and below 20 ˚C at the other end
63 of the greenhouse (Supplementary Information 1). Thus, pots growing near the heater were
64 exposed to higher temperatures for the entire three-month duration of the experiment.

65 The experiment was ended when the first plants started to initiate flowers (10 weeks after
66 the start of the experiment). During the last two days of the experiment we measured the soil
67 CO_2 efflux (SCE), using a closed dynamic infrared gas analysis system, consisting of a home-
68 made soil chamber (10.2 cm diameter, 12.3 cm height) and a Li-6200 (LICOR Inc, Nebraska,
69 USA). Attached in parallel to the system was a two-litre stainless steel collector to collect air
70 samples for isotopic analysis. The airflow through the system was diverted through this collector
71 when taking air samples for isotope analysis. During flux measurements, the collector was
72 always by-passed. The soil chamber was equipped with a pressure equilibration tube (0.76 mm
73 inner diameter, 0.7 m long) to mitigate potential pressure gradients. Diffusion of CO_2 through
74 this tube was negligible because during the measurements the CO_2 concentration difference
75 between the chamber headspace and the atmosphere went from –25 to +25 ppm. Inside the soil
76 chamber, air was mixed with a horizontally blowing fan mounted on the top of the chamber. Fan
77 speed was reduced so that air speed near the soil surface was < 0.1 m s^{-1}.

78 All measurements were made within two consecutive days and in a predetermined
79 random order. Furthermore, each pot was measured twice when the flux rates differed less than
80 5%. In case of larger differences, we made two extra measurements (immediately after the first

two measurements) and used the mean of the four fluxes as the final value. Estimates of R_{SOM} and R_{rhizo} were based on the difference in $\delta^{13}C$ between the C_3 plant-derived organic matter ($\delta^{13}C$ around -25‰) and the C_4 maize root-derived carbon (circa -14‰). We calculated R_{SOM} and R_{rhizo} with a basic mixing equation (Balesdent *et al.*, 1987):

$$R_{SOM} = SCE^* (\delta^{13}C_{SCE} - \delta^{13}C_{Rrhizo})/(\delta^{13}C_{RSOM} - \delta^{13}C_{Rrhizo}), \quad (1)$$

where SCE is the measured soil CO_2 efflux, $\delta^{13}C_{SCE}$ is the isotopic signature of the soil-respired CO_2 and $\delta^{13}C_{RSOM}$ and $\delta^{13}C_{Rrhizo}$ are the isotopic signatures of the soil carbon-derived CO_2 and the root carbon-derived CO_2, respectively. Rhizosphere respiration was estimated as the difference between SCE and R_{SOM}. Detailed information on the partitioning method is given in Supplementary Information 1. In figure 1, we demonstrate that R_{rhizo} increased with increasing root biomass, which substantiates the methodology of our separation technique.

Figure 1

Regressions of SCE, R_{SOM} and R_{rhizo} versus soil temperature were fitted in Matlab (7.2.0.232, The Mathworks, Natick, MA, USA). Further statistical analyses were performed in SAS (SAS system 9.2, SAS Institute, Cary, NC, USA). We used two-way Ancova analysis, with soil temperature as a covariable, to test for fertilization and plant density effects on the temperature responses of SCE, R_{SOM} and R_{rhizo}. Soil temperature data are shown in Table 1.

Table 1

Soil respiration significantly increased with growth temperature, but this increase was solely due to the temperature response of R_{SOM}, as R_{rhizo} did not change with growth temperature (Fig. 2). The decreasing temperature response of SCE with increasing plant density (Table 2), and thus with increasing contribution of R_{rhizo} to SCE, further confirmed that R_{rhizo} was less sensitive to growth temperature than R_{SOM} and adds additional support to our methodology. Similarly, Heinemeyer et al. (2007) found that heterotrophic respiration was the main process responsible for the exponential relation between SCE and temperature. We further observed that, although both plant density and fertilization significantly affected root biomass (Supplementary Information 2) and thus R_{rhizo}, the temperature response of R_{rhizo} remained unaffected (Table 2).

Increased labile soil carbon inputs with increasing root biomass could affect the temperature response of R_{SOM} (Davidson & Janssens 2006), but this was not the case in our experiment where the response of R_{SOM} to growth temperature was unaffected by plant density (Table 2). Possibly, soil microbes were not carbon-limited, in which case additional substrate supply would not alter the temperature response of R_{SOM}. Alternatively, the additional labile soil carbon in the high density pots was utilized in the weeks before our measurements. The latter is supported by the measurements of soil organic carbon content, showing no difference among the treatments (Supplementary Information 2).

Table 2

Figure 2

The obvious zero-effect of growth temperature on R_{rhizo} suggests full thermal acclimation, which was clearly not the case for R_{SOM} (although we cannot exclude the possibility

of partial acclimation of R_{SOM}). Several studies have reported thermal acclimation of autotrophic respiration (e.g., Rook 1969; Bryla *et al.* 1997; Atkin *et al.* 2000; Atkin *et al.* 2005; Ow *et al.* 2008). Whereas in plants thermal acclimation allows the maintenance of a positive carbon balance (Atkin & Tjoelker 2003), for soil microorganisms, there is no obvious benefit of reduced activity with increasing temperature. Accordingly, the decreased effect of warming on microbial respiration, which frequently follows an initial positive warming effect (Hyvönen *et al.* 2007), is believed to be caused primarily by substrate depletion (Kirschbaum 2004; Eliasson *et al.* 2005; Hartley *et al.* 2007b; Vicca *et al.* 2009). In the absence of substrate limitations, microbial activity might even increase more than expected from its intrinsic temperature sensitivity (Hartley *et al.* 2008).

In conclusion, we demonstrated different effects of growth temperature on R_{rhizo} versus R_{SOM}. In this particular study, R_{rhizo} was even insensitive to differences in growth temperature. We thus suggest that different temperature response mechanisms for R_{rhizo} and R_{SOM} must be taken into account when modelling respiration in terrestrial ecosystems. This is particularly important because it is the change in long-lived soil carbon stocks that determines whether terrestrial ecosystems will rather mitigate or exacerbate climatic change.

Acknowledgements

We acknowledge Sue Wood and Joe Cali for chemical analyses and Werner Kutsch for scientific discussions. We thank the ANU for the use of the glasshouse and taking care of the plants. SV holds a grant from the Institute for Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen). IAJ acknowledges the Fund for Scientific Research – Flanders for financial support.

Tables

Table 1: Soil temperature (°C) of all replicates for the different plant densities (D=1: one plant per pot, D=3: three plants per pot; D=6: six plant per pot) and for unfertilized (UF) and fertilized (F) pots. Note that one outlier value for the soil CO_2 efflux (D=6, F) was removed from the analyses.

	Replica	D=1	D=3	D=6
	1	18	19.5	19
	2	22.2	22.3	20
	3	23	23.9	21.7
UF	4	24.7	24.9	22.15
	5	24.75	25.2	23.75
	6	27.5	28.1	26.7
	7		28.5	27.5
	8	21.7	21.3	24.2
	9	21.7	22.7	25.6
	10	21.8	24.45	26.3
F	11	23.6	24.9	27.2
	12	27.5	26.1	
	13	28.5	26.3	
	14		27.45	

Table 2: The response to growth temperature (expressed as Q_{10}) of soil CO_2 efflux (SCE), soil organic matter decomposition (R_{SOM}) and rhizosphere respiration (R_{rhizo}) for the different plant densities (D=1: one plant per pot, D=3: three plants per pot; D=6: six plant per pot) and for unfertilized (UF) and fertilized (F) pots. These Q_{10} values were computed by fitting the function SCE, R_{rhizo} or R_{SOM} = $a*Q_{10}^{(T-10)/10}$, where a and Q_{10} are estimated parameters and T is soil temperature) We also present the results of the Ancova analysis for testing density and fertilization effects on the temperature responses of SCE, R_{SOM} and R_{rhizo}; D, F and D*F represent the p values for the density, fertilization and density*fertilization interaction effect, respectively.

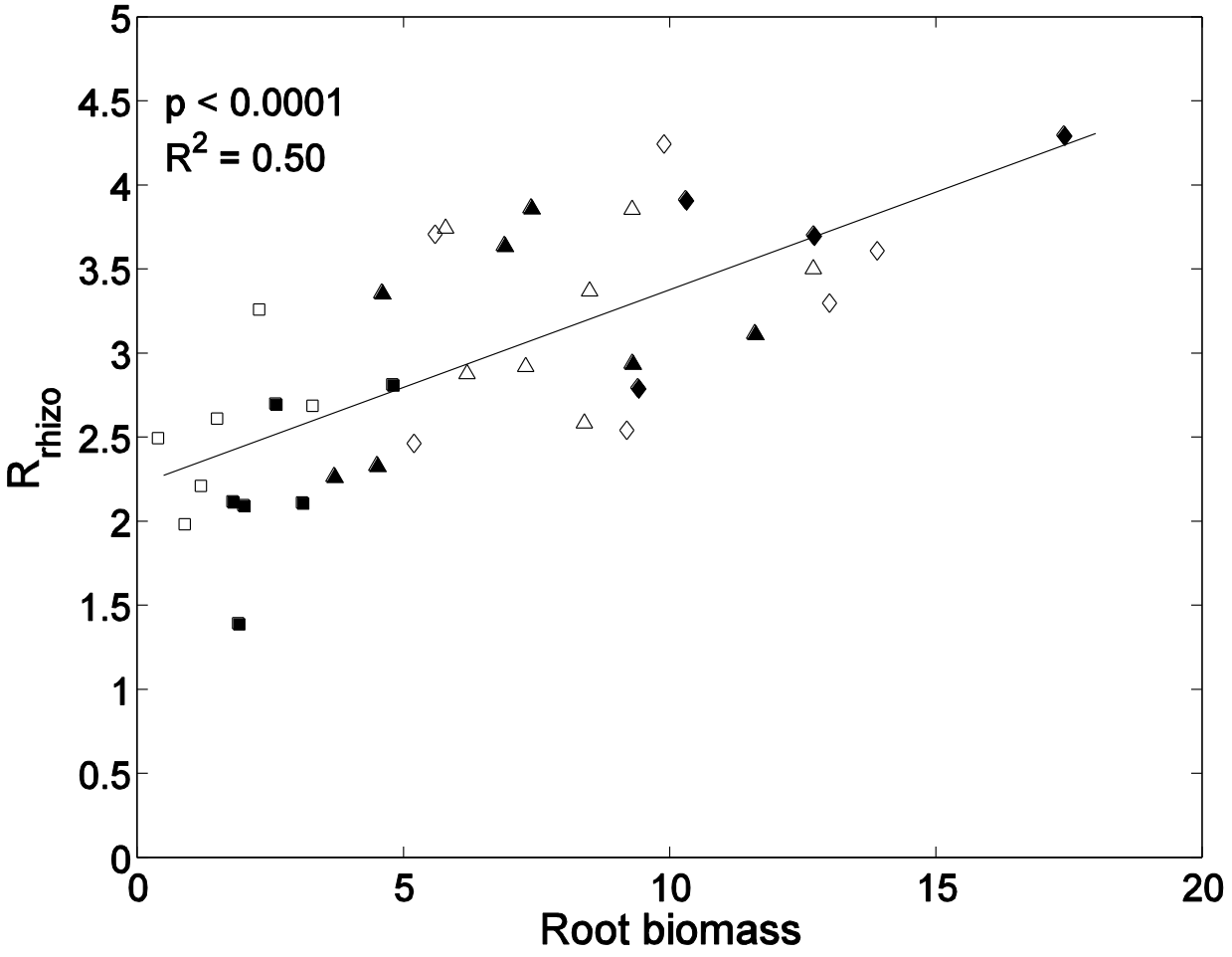
					P values (Ancova)		
		D=1	D=3	D=6	D	F	D*F
SCE	UF	2.06	1.56	1.13	0.06	0.32	0.04
	F	1.42	1.52	0.92			
R_{SOM}	UF	3.43	2.87	2.38	0.57	0.59	0.53
	F	2.43	2.52	2.67			
R_{rhizo}	UF	1.20	1.04	0.86	0.71	0.22	0.19
	F	0.66	1.04	0.43			

Figures

Figure 1: Rhizosphere respiration (R_{rhizo}; µmol CO_2 m^{-2} s^{-1}) versus root biomass (g pot^{-1}). White and black symbols represent the unfertilized and fertilized treatment, respectively. Squares are pots with one plant, triangles are pots with three plants and diamonds represent pots with six plants. The line represents the linear regression fitted through the data, and the p value indicates the significance of this regression. The high R_{rhizo} at zero root biomass probably indicates the fraction of rhizosphere that remains in the soil when roots are extracted.

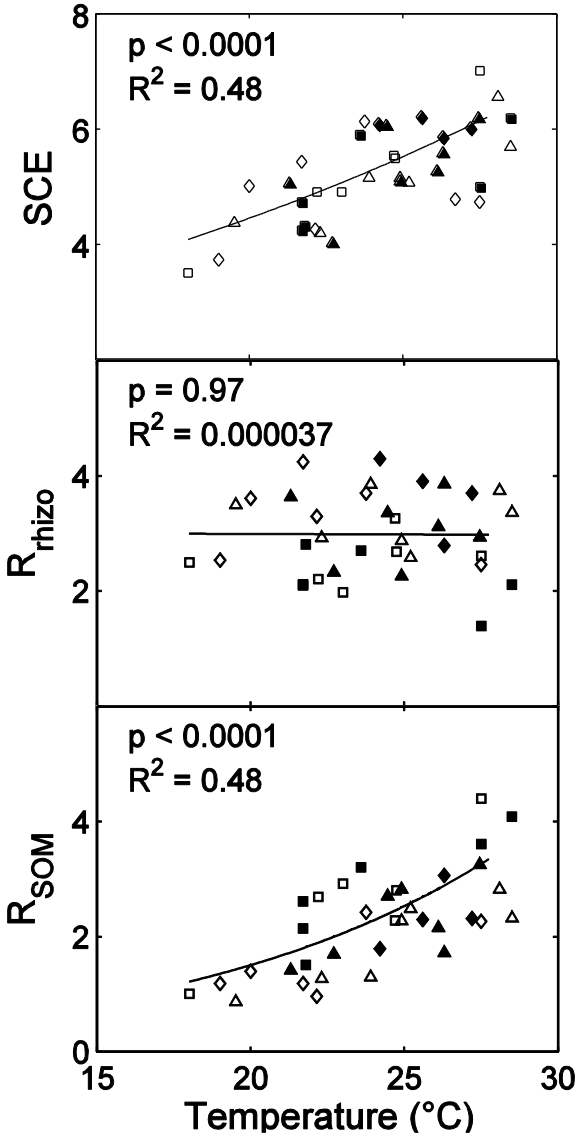
Figure 2: Soil CO_2 efflux (SCE; µmol CO_2 m^{-2} s^{-1}), rhizosphere respiration (R_{rhizo}; µmol CO_2 m^{-2} s^{-1}) and soil organic matter decomposition (R_{SOM}; µmol CO_2 m^{-2} s^{-1}) versus soil temperature. The p value indicates the significance of the fitted regression (SCE, R_{rhizo} or $R_{SOM} = a*b^{(T-10)/10}$, where a and b are estimated parameters and T is soil temperature). White and black symbols represent the unfertilized and fertilized treatment, respectively. Squares are pots with one plant, triangles are pots with three plants and diamonds represent pots with six plants.

181 **Figure 1:**



182

183 **Figure 2:**



184

185 **References**

186

187 Atkin O.K., Bruhn D., Hurry V.M. & Tjoelker M.G. (2005). The hot and the cold: unravelling the variable
188 response of plant respiration to temperature. *Functional Plant Biology*, 32, 87-105.
189 Atkin O.K., Edwards E.J. & Loveys B.R. (2000). Response of root respiration to changes in temperature
190 and its relevance to global warming. *New Phytologist*, 147, 141-154.
191 Atkin O.K. & Tjoelker M.G. (2003). Thermal acclimation and the dynamic response of plant respiration to
192 temperature. *TRENDS in Plant Science*, 8, 343-351.
193 Baath E. & Wallander H. (2003). Soil and rhizosphere microorganisms have the same Q(10) for
194 respiration in a model system. *Global Change Biology*, 9, 1788-1791.
195 Bhupinderpal-Singh, Nordgren A., Lofvenius M.O., Hogberg M.N., Mellander P.E. & Hogberg P. (2003).
196 Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest:
197 extending observations beyond the first year. *Plant Cell Environ.*, 26, 1287-1296.
198 Boone R.D., Nadelhoffer K.J., Canary J.D. & Kaye J.P. (1998). Roots exert a strong influence on the
199 temperature sensitivity of soil respiration. *Nature*, 396, 570-572.
200 Bryla D.R., Bouma T.J. & Eissenstat D.M. (1997). Root respiration in citrus acclimates to temperature and
201 slows during drought. *Plant, Cell and Environment*, 20, 1411-1420.
202 Curiel Yuste J., Janssens I.A., Carrara A. & Ceulemans R. (2004). Annual Q10 of soil respiration reflects
203 plant phenological patterns as well as temperature sensitivity. *Global Change Biology*, 10, 161-
204 169.
205 Davidson E.A. & Janssens I.A. (2006). Temperature sensitivity of soil carbon decomposition and
206 feedbacks to climate change. *Nature*, 440, 165-173.
207 Davidson E.A., Janssens I.A. & Luo Y. (2006). On the variability of respiration in terrestrial ecosystems:
208 moving beyond Q_{10}. *Global Change Biology*, 12, 154-164.
209 Eliasson P.E., McMurtrie R.E., Pepper D.A., Strömgren M., Linder S. & Agren G.I. (2005). The response of
210 heterotrophic CO2 flux to soil warming. *Global Change Biology*, 11, 167-181.
211 Hartley I.P., Heinemeyer A., Evans S.P. & Ineson P. (2007a). The effect of soil warming on bulk soil vs.
212 rhizosphere respiration. *Global Change Biology*, 13, 2654-2667.
213 Hartley I.P., Heinemeyer A. & Ineson P. (2007b). Effects of three years of soil warming and shading on
214 the rate of soil respiration: substrate availability and not thermal acclimation mediates observed
215 response. *Global Change Biology*, 13, 1761-1770.
216 Hartley I.P., Hopkins D.W., Garnett M.H., Sommerkorn M. & Wookey P.A. (2008). Soil microbial
217 respiration in arctic soil does not acclimate to temperature. *Ecology Letters*, 11, 1092-1100.
218 Heinemeyer A., Hartley I.P., Evans S.P., De la Fuente J.A.C. & Ineson P. (2007). Forest soil CO2 flux:
219 uncovering the contribution and environmental responses of ectomycorrhizas. *Global Change*
220 *Biology*, 13, 1786-1797.
221 Hyvönen R., Ågren G.I., Linder S., Persson T., Cotrufo M.F., Ekblad A., Freeman M., Grelle A., Janssens
222 I.A., Jarvis P.G., Kellomaki S., Lindroth A., Loustau D., Lundmark T., Norby R.J., Oren R., Pilegaard
223 K., Ryan M.G., Sigurdsson B.D., Stromgren M., van Oijen M. & Wallin G. (2007). The likely impact
224 of elevated [CO2], nitrogen deposition, increased temperature and management on carbon
225 sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist*,
226 173, 463-480.
227 Kirschbaum M.U. (2004). Soil respiration under prolonged soil warming: are rate reductions caused by
228 acclimation or substrate loss? *Global Change Biology*, 10, 1870-1877.
229 Kuzyakov Y. (2006). Sources of CO_2 efflux from soil and review of partitioning methods. *Soil Biology and*
230 *Biochemistry*, 38, 425-448.

231 Moyano F.E., Kutsch W.L. & Schulze E.D. (2007). Response of mycorrhizal, rhizosphere and soil basal
232 respiration to temperature and photosynthesis in a barley field. *Soil Biol. Biochem.*, 39, 843-853.
233 Ow L.F., Griffin K.L., Whitehead D., Walcroft A.S. & Turnbull M.H. (2008). Thermal acclimation of leaf
234 respiration but not photosynthesis in Populus deltoides x nigra. *New Phytologist*, 178, 123-134.
235 Rook D.A. (1969). The influence of growing temperature on photosynthesis and respiration of *Pinus*
236 *radiata* seedlings. *New Zealand Journal of Botany*, 7, 43-55.
237 Schindlbacher A., Zechmeister-Boltenstern S. & Jandl R. (2009). Carbon losses due to soil warming: Do
238 autotrophic and heterotrophic soil respiration respond equally? *Global Change Biology*.
239 Vicca S., Fivez L., Kockelbergh F., Van Pelt D., Segers J.R., Meire P., Ceulemans R. & Janssens I.A. (2009).
240 No signs of thermal acclimation of heterotrophic respiration from peat soils exposed to different
241 water levels. *Soil Biol. Biochem.*, 41, 2014-2016.
242
243