10 Forum L

Letters



Fig. 1 Relations between the autotrophic and heterotrophic components of soil respiration and soil temperature (at a soil depth of 5 cm) in a boreal pine forest (data from Bhupinderpal-Singh *et al.*, 2003). Measurements from the beginning (17 May 2001) to the end (12 October 2001) of the season are numbered consecutively (1–8). The red arrows show the responses to a decline in soil temperature in the middle of the summer.

respiration is also driven by the strong seasonality in tree belowground C allocation.

Peter Högberg

Department of Forest Ecology and Management, SLU, SE-901 83 Umeå, Sweden (tel +46 786 8353; email peter.hogberg@sek.slu.se)

References

- Bååth E, Wallander H. 2003. Soil and rhizosphere organisms have the same Q₁₀ for respiration in a model system. *Global Change Biology* 9: 1788–1791.
- Bhupinderpal-Singh, Nordgren A, Ottosson-Löfvenius M, Högberg MN, Mellander P-E, Högberg P. 2003. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant, Cell & Environment* 26: 1287– 1296.

- Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* **396**: 570–572.
- Hansen J, Türk R, Vogg G, Heim R, Beck E. 1997. Conifer carbohydrate physiology: updating classical views. In: Rennenberg H, Eschrich W, Ziegler H, eds. *Trees – contributions to modern tree physiology*. Leiden, the Netherlands: Backhuys, 97–108.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA. 2000. Separating root and microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48: 115–146.
- Heinemeyer A, Hartley IP, Evans SP, Carreira de la Fuentes JA, Ineson P. 2007. Forest soil CO₂ flux: uncovering the contribution and environmental responses of ectomycorrhizas. *Global Change Biology* 13: 1786–1797.
- Högberg MN, Briones MJI, Keel SG, Metcalfe DB, Campbell C,
 Midwood AJ, Thornton B, Hurry V, Linder S, Näsholm T *et al.* 2010.
 Quantification of effects of season and nitrogen supply on tree
 below-ground carbon transfer to ectomycorrhizal fungi and other soil
 organisms in a boreal pine forest. *New Phytologist* 187: 485–493.
- Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411: 789–792.
- Raich JW, Schlesinger WH. 1992. The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Series B* 44: 81–99.
- Yuste JC, Janssens IA, Carrara A, Ceulemans R. 2004. Annual Q₁₀ of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology* 10: 161–169.
- Zhou X, Luo Y, Gao C, Verburg PSJ, Arnone JA III, Darrouzet-Nardi A, Schimel DS. 2010. Concurrent and lagged impacts of an anomalously warm year on autotrophic and heterotrophic components of soil respiration: a deconvolution analysis. *New Phytologist* 187: 184–198.

Key words: autotrophic respiration, boreal forests, heterotrophic respiration, seasonality, temperate forests, temperature sensitivity.

Deconvolution analysis to quantify autotrophic and heterotrophic respiration and their temperature sensitivities

Högberg (2010) has highlighted one of the most important confounding processes – seasonal dynamics of carbon substrate supply – in quantification of the temperature sensitivity of soil respiration. He is also a leading scientist who has made great contributions to this issue using innovative methods of tree girdling and isotope tracing. Tree girdling is an effective method that is used to manipulate substrate supply and enables scientists to separate autotrophic (R_A) from heterotrophic (R_H) components of soil respiration. Similar methods that manipulate substrate supply include clipping and shading in grasslands (e.g. Wan & Luo, 2003), clear-cutting in forests (e.g. Ohashi *et al.*, 2000), trenching (e.g. Jiang *et al.*, 2005), gap formation (e.g. Brumme, 1995) and root removal (e.g. Wiant, 1967). These methods usually alter physical and/or microclimate environments, which may compromise the accuracy of separating R_A and R_H . Carbon isotopes can be used to trace pathways of photosynthate in an ecosystem while having little effect on the environment (Högberg *et al.*, 2010). However, isotope tracing is not always possible in all ecosystems, for reasons of cost and/or access to different isotopic sources.

We developed and applied the deconvolution method not only to separate R_A from R_H of soil respiration data but also to estimate various parameters that would enable us to estimate the temperature sensitivity of R_A and R_H . Deconvolution is a method used to separate measured soil respiration into source components, such as root respiration, litter decomposition and oxidation of soil organic matter (SOM). As each of the source components shows different kinetic rates of transfer of carbon from plant, litter and SOM to the atmosphere, the method differentiates those source components according to the kinetic rates (Luo et al., 2001). Our analysis estimated carbon transfer among 10 pools, together with parameters that represent moisture and temperature regulation of those transfer rates from measured soil respiration using a probabilistic inversion technique (Zhou et al., 2010). We then estimated R_A from carbon transfer from the root pool and $R_{\rm H}$ from carbon transfer from litter, microbial and SOM pools. We estimated the temperature sensitivity of $R_{\rm H}$ via deconvolution and found insignificant effects by warming and posttreatment. We did not directly estimate the temperature sensitivity of R_A but showed indirectly that R_A was more sensitive to warming than R_H, as we hypothesized. Overall, deconvolution is a mathematical approach used not only to eliminate confounding factors but also directly to quantify the temperature sensitivities of various source components.

Dr Högberg is very clever to take advantage of the summer cold period of 20 d to illustrate the temperature sensitivity of R_A . If the red arrow in Fig. 1 of Högberg (2010) truly represents the sensitivity of R_A to changes in temperature, R_A would show a slight decrease as the temperature increases, which does not seem to be realistic. The insensitivity of R_A during that short period must result from other processes, such as lagged effects, the very subject of our study, instead of the direct evidence of lower temperature sensitivity of R_A , as claimed by Högberg (2010). Overall, the data in Fig. 1 of Högberg's letter do show a steeper increase with soil temperature for R_A than R_H over the whole period of measurement. His data can be analyzed using deconvolution with internal logical consistency towards understanding source components and their temperature sensitivity.

Yiqi Luo and Xuhui Zhou*

Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA (*Author for correspondence: tel +1 405 325 8578; email zxuhui14@ou.edu)

References

- Brumme R. 1995. Mechanisms of carbon and nutrient release and retention in beech forest gaps. 3. Environmental-regulation of soil respiration and nitrous-oxide emissions along a microclimatic gradient. *Plant and Soil* 169: 593–600.
- Högberg MN, Briones MJI, Keel SG, Metcalfe DB, Campbell C, Midwood AJ, Thornton B, Hurry V, Linder S, Näsholm T et al. 2010. Quantification of effects of season and nitrogen supply on tree belowground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytologist* 187: 485–493.
- Högberg P. 2010. Is tree root respiration more sensitive than heterotrophic respiration to changes in soil temperature? *New Phytologist* 188: 9–10.
- Jiang LF, Shi FC, Li B, Luo YQ, Chen JQ, Chen JK. 2005. Separating rhizosphere respiration from total soil respiration in two larch plantations in northeastern China. *Tree Physiology* 25: 1187–1195.
- Luo YQ, Wu LH, Andrews JA, White L, Matamala R, Schafer KVR, Schlesinger WH. 2001. Elevated CO₂ differentiates ecosystem carbon processes: deconvolution analysis of Duke Forest FACE data. *Ecological Monographs* 71: 357–376.
- Ohashi M, Gyokusen K, Saito A. 2000. Contribution of root respiration to total soil respiration in a Japanese cedar (*Cryptomeria japonica* D. Don) artificial forest. *Ecological Research* 15: 323–333.
- Wan SQ, Luo YQ 2003. Substrate regulation of soil respiration in a tallgrass prairie: results of a clipping and shading experiment. *Global Biogeochemical Cycles* 17: 1054, doi:10.1029/2002GB001971.
- Wiant HV. 1967. Contribution of roots to forest soil respiration. Advancing Frontiers of Plant Sciences 18: 163–167.
- Zhou XH, Luo YQ, Gao C, Verburg PSJ, Arnone JA, Darrouzet-Nardi A, Schimel DS. 2010. Concurrent and lagged impacts of an anomalously warm year on autotrophic and heterotrophic components of soil respiration: a deconvolution analysis. *New Phytologist* 187: 184– 198.

Key words: carbon, deconvolution method, isotope tracing, respiration, tree girdling.