

Letter to the Editor

Response to the comments by Peter Höglberg, Nina Buchmann and David J. Read on the review ‘Sources of CO₂ efflux from soil and review of partitioning methods’ (Soil Biology & Biochemistry 38, 425–448)

Object- versus method-oriented terminology

The comments by Prof. Peter Höglberg, Prof. Nina Buchmann, and Prof. David J. Read on my review ‘Sources of CO₂ efflux from soil and review of partitioning methods’ (Kuzyakov, 2006) were mainly focused on my criticism of the term ‘autotrophic respiration’ that was frequently used in CO₂ partitioning studies.

The term ‘autotrophic respiration’ was often applied for the sum of root respiration and respiration of rhizosphere-associated microorganisms. In contrast, the term ‘heterotrophic respiration’ was applied to describe microbial decomposition of dead plant material and soil organic matter. In the recent review “Sources of CO₂ efflux from soil and review of partitioning methods”, I presented some discrepancies in such a definition of ‘autotrophic respiration’, because it includes the respiration of many heterotrophic organisms using carbon-rich substrates released by roots. Therefore, I suggested that the term ‘respiration by autotrophs’ should include only root respiration per se.

The main matter concerning the terms is: should the terminology be limited by the existing methods or be defined based on the nature of the objects?

In their comments, Höglberg et al. (2006) pointed out (i) the absence of sharp boundaries between root and rhizomicrobial respiration, (ii) the importance of mycorrhizal fungi, and (iii) the methodical difficulties due to the separation of these two CO₂ sources as the main reasons to lump root respiration with rhizomicrobial respiration to one term ‘autotrophic respiration’.

1. I clearly see the gradual transition between the root respiration per se and respiration of rhizosphere-associated microorganisms, the importance of mycorrhizal fungi, as well as many methodical problems in the separation of the respiration of autotrophic and heterotrophic organisms, especially under field conditions.

In my opinion, however, the energy source for the organisms should be considered as the main determinant of the respiration of autotrophs and heterotrophs, and not the transition uncertainty or methodical problems. It should be remembered that the terms ‘autotrophic’ or

‘heterotrophic’ show the principle of organic substance acquisition by organisms and are not connected with the respiration. Therefore, I suggested the use of ‘respiration by autotrophs’ and ‘respiration by heterotrophs’ or according to Bond-Lamberty et al. (2004) ‘heterotrophic and autotrophic components of soil respiration’.

2. I fully agree with the comment by Höglberg et al. (2006) that for ecosystem ecologists estimating the contribution of ecosystems (partially soils) to changes of atmospheric CO₂ concentration, it is mainly important to separate the SOM-derived and root-derived CO₂ (I also underlined this in the Abstract and in section 2.5 of the review). However, the ecosystem approach should also consider the carbon and energy fluxes between the plant and rhizosphere organisms. Despite short turnover times, the rhizodeposits are energy rich and easily available C substrates for microorganisms, driving the most intensive C turnover processes in soils. Therefore, the lumping of CO₂ fluxes from rhizodeposits’ decomposition with the energy-poor CO₂ of root respiration would mix substantially and functionally different C fluxes and neglect the contribution of rhizodeposition to the belowground life and turnover of soil organic matter.
Besides litter, rhizodeposition and root turnover remain in most ecosystems, including forests, the main primary energy and carbon source for most soil microorganisms. Thus, by accepting the respiration of rhizosphere organisms as ‘autotrophic respiration’, we will neglect the main carbon and energy input by living plants into the soil.
3. I agree with the comment by Höglberg et al. (2006) that the combination of root respiration per se and rhizomicrobial respiration is a pragmatic approach used in many other studies (e.g., Hanson et al., 2000). It is very positive that in all publications by Prof. Höglberg and Prof. Buchmann’s research groups, clear definitions of the CO₂ sources contributing to the ‘autotrophic respiration’ (and other CO₂ sources) were presented. In contrast, in many publications by some other authors, the terms ‘autotrophic respiration’ and ‘root respiration’ are frequently not clarified and tacitly included the respiration of heterotrophic microorganisms. This stands out against the term ‘root respiration’ used, e.g., in plant physiology. Such absence of clear source definitions confounds the results and methods, complicating the transferability between the studies and disciplines.

- As noted in the comments by Högberg et al. (2006) on the term ‘autotrophic respiration’ “...many other soil microbiologists feel uncomfortable with this idea of lumping together root respiration, with the respiration by what is taxonomically regarded as heterotrophic microorganisms”: this is the main point, that the terminology should be transparent and transferable between the sciences regardless of whether the study was conducted on the level of micro-sites or ecosystem scale.
4. Concerning the processes leading to the CO₂ efflux from these two sources, mainly sucrose is used for root respiration. In contrast, the respiration of rhizosphere microorganisms involves not only the decomposition of sucrose transferred from roots to the mycorrhizal fungi. Many other microorganisms’ groups decompose not only sucrose, but also other sugars including mucigel polysaccharides, as well as carboxylic acids and amino acids released by the roots as exudates. The rhizosphere respiration also includes microbial decomposition of hyphens of mycorrhizal fungi, as well as the decomposition of fine and medium roots, root hairs, etc. The previous meaning of the term ‘autotrophic respiration’ disregards the existence and the importance of these organisms and these C sources that are crucial for the ecosystem functions.
 5. It is also important to note that environmental variables controlling root respiration may differ from those controlling rhizomicrobial respiration. The root respiration per se increases with increasing temperature, nutrient supply, salinity, irradiance, CO₂ partial pressure, and pH decrease (Lambers et al., 1998, pp. 114–121). The specific respiration of young growing roots is higher compared to older roots. In contrast, the rhizomicrobial respiration is mainly resource limited, which means it is driven not by temperature, but by the amount of rhizodeposits inclusive exudates. The amount of rhizodeposits depends on the physiological state of the roots and may be higher for older roots. The amount of exudates per root mass unit is higher for young roots and depends on the photosynthesis intensity, which means it is driven by light intensity and water availability. Since the variables controlling root respiration differ from those of rhizomicrobial respiration, this should be considered at least in process-based models. The partitioning of root and rhizomicrobial respiration may be a fascinating issue, especially in the studies of global climate change effects on CO₂ fluxes from soil because in contrast to the resource-limited rhizomicrobial respiration, the root respiration acclimates very quickly to factors such as elevated temperature (Lambers et al., 1998, p. 119). Also, if we want to “...create a ‘theory’ of respiration that allows us to predict how it may change in the next century...” (Trumbore, 2006), clear definitions of pools and fluxes, as well as their controlling variables, are necessary.
 6. As noted in the review by Killham and Yeomans (2001) and in my contribution (Kuzyakov, 2006), the separation of root and rhizomicrobial respiration may be the next step in the partitioning of CO₂ fluxes. This will contribute to the better understanding of belowground processes and interrelationships between plants and soil microorganisms. It will also allow for the quantitative estimation of C input by plants into the soil (including C flux from plant to fungus) and link rhizosphere processes with ecosystem fluxes. In my review, physical separation of the roots and ectomycorrhizal fungi was never suggested and I fully agree with the comment by Högberg et al. (2006) that “Any attempt to physically separate the two sources of respiration would inevitably disrupt the autotrophically driven C flux from plant to the fungus.”
- Even though the separation of root and rhizomicrobial respiration is difficult and probably impossible under field conditions, I think that the terminology should be based not on the possibilities of the methods of today, but on the nature of the objects. Such object-oriented terminology is process aimed and will challenge the development of new methods.
- Lastly, there is no doubt that the main aim of all our studies and discussions is not the terminology itself, but the substantial progress in process’ understanding, e.g., partitioning of CO₂ fluxes and quantitative evaluation of individual CO₂ sources in various ecosystems. I am always delighted by the studies and ideas of Prof. Högberg, Prof. Buchmann, and Prof. Read’s research groups, which not only strongly contributed to the matter of CO₂ fluxes partitioning and understanding of processes under field conditions, but also primed a great number of subsequent investigations.

References

- Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration?. *Global Change Biology* 10, 1756–1766.
- Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48, 115–146.
- Högberg, P., Buchmann, N., Read, D.J., 2006. Comments on Yakov Kuzyakov’s review ‘Sources of CO₂ efflux from soil and review of partitioning methods’. *Soil Biology and Biochemistry*, this issue.
- Killham, K., Yeomans, C., 2001. Rhizosphere carbon flow measurement and implications: from isotopes to reporter genes. *Plant and Soil* 232, 91–96.
- Lambers, H., Chapin III, F.S., Pons, T.L., 1998. *Plant Physiological Ecology*. Springer, New York.
- Kuzyakov, Y., 2006. Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry* 38, 425–448.
- Trumbore, S., 2006. Carbon respired by terrestrial ecosystems—recent progress and challenges. *Global Change Biology* 12, 141–153.

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