УДК 581.52(510) © **2010**

EFFECT OF ASSIMILATE SUPPLY ON SOIL RESPIRATION IN A FOREST-STEPPE ECOTONE, NORTHERN CHINA

ВЛИЯНИЕ ПРИВНОСА АССИМИЛЯНТОВ НА ПОЧВЕННОЕ ДЫХАНИЕ В ЭКОСИСТЕМАХ ЛЕСОСТЕПНОГО ЭКОТОНА СЕВЕРНОГО КИТАЯ

W. WANG

Department of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, 100871, China Fax: +8610 627–565–60; e-mail: wangw@urban.pku.edu.cn

Soil respiration (SR) is the primary pathway by which plant-fixed CO_2 is released back to the atmosphere. Recent studies suggested that aboveground photosynthesis activity may affect as strongly as or more strongly on SR than soil temperature. We conducted a preliminary study to explore the effect of short-term assimilate supply on SR and to estimate the contribution of root-derived respiration to SR across 6 ecosystems in a foreststeppe ecotone, north China.

Key words: assimilate supply, soil respiration, clipping, trenching.

Почвенное дыхание является основным путем, которым фиксированный растениями CO₂ возвращается в атмосферу. В результате недавних исследований было выдвинуто предположение, что надземная фотосинтетическая активность может влиять на почвенное дыхание настолько же сильно, или даже еще сильнее, чем температура почвы. На примере 6 экосистем лесостепного экотона в Северном Китае, нами проведено предварительное исследование, задачей которого было установить эффект кратковременного привноса ассимилянтов на почвенное дыхание, и оценить вклад корневого дыхания растений в интенсивность почвенного дыхания.

Ключевые слова: запас органических веществ, почвенное дыхание, срезка наземной фитомассы, изоляция подземной фитомассы.

INTRODUCTION

Soil respiration (SR) is the primary pathway for CO₂ fixed by plants returning to the atmosphere (Hugberg, Read, 2006; Bond-Lamberty, Thomon, 2010), consisting of respiration from autotrophic roots (and mycorrhizal fungi) and heterotrophic microorganisms. The global CO₂ flux from soils is estimated to be within the range of 64–72 Gt C y⁻¹, accounting for 20–38 % of annual input of CO₂–C to the atmosphere from terrestrial and marine sources (Raich, Schlesinger, 1992), and is therefore an important regulator of climate change as well as determinant of net ecosystem C balance (Rustad et al., 2000).

The studies of SR have attracted substantial concern during the past decade, but SR is frequently considered as an isolated belowground process until recent findings showed that SR coupled belowground with aboveground C cycling processes (Hugberg et al., 2001; Kuzyakov, Cheng, 2001; Wan, Luo, 2003). The well-documented temperature dependence of SR has been challenged and several recent studies suggested that aboveground photosynthesis activity may affect as strongly as or more strongly on SR than soil temperature (Janssens et al., 2001; Kuzyakov, Cheng, 2001; Bhupinderpal-Singh et al., 2003). For example, SR was observed to positively correlate with aboveground net primary productivity in grassland and litter production in forests, which are related to the quantity of C supplied to soil (Raich, Schlesinger, 1992; Luo et al., 1996; Raich, Tufekcioglu, 2000).

Many recent studies have shown the connection between photosynthetic activity and SR by analyzing the isotopic signature of assimilated and respired carbon (Andrews et al., 1999; Ekblad, Hugberg, 2001), relating gross primary productivity or cumulated radiation flux and respiration rates (Moyano et al., 2008), clipping (Bahn et al., 2006), shading (Wan, Luo, 2003), trenching (Boone et al., 1998) and girdling (Hugberg et al., 2001, 2009). However, the conclusions about the response of SR to short-term assimilate supply were mixed. For instance, for C₄-dominated grassland, SR was observed to decrease by 21-49 % in a Kansas steppe (Bremer et al., 1998) and by 19 % in a Minnestota steppe (Craine et al., 1999) after clipping. Whilst in a C₃-dominated meadow sites, clipping caused an increase of both soil and root respiration, due to an increase in soil temperature on the clipped plots (Bahn et al., 2006). Therefore, the effects of short-term assimilate supply on soil and root respiration is still required to investigate across different ecosystems.

Another major uncertainty connected with the factors controlling SR is constrained by the challenge of apportioning sources of CO_2 between root-derived (autotrophic roots and mycorrhizal fungi) and heterotrophic microorganisms (Binkley et al., 2006; Wang, Fang, 2009). Increases in root-derived respiration (RR) may reflect increased C inputs to the soil through photosynthesis, specific root activity, or root biomass (Hugberg et al. 2001), whereas increased heterotrophic respiration may reduce the potential for C storage in the soil (Grace, 2004). Thus quantifying the components of SR is vital for the prediction of ecosystem response to climate change, and for understanding the nature and extent of feedbacks between climate change and soil processes, and incorporating the components of SR into climate change models separately (Baggs, 2006). The reported contribution of RR to SR varied within a wide range (Hanson et al., 2000; Raich, Tufekcioglu, 2000; Bond-Lamberty et al., 2004). Although some of this variability reflects diversity of the studied types of soils and ecosystems, a considerable proportion of it probably originates from the variety of measurement techniques used (Kuzyakov, 2006; Subke et al., 2006; Marsden et al., 2008). The comparisons in the contribution of RR to SR among different ecosystems were rarely determined using the same method.

In this study, we conducted a preliminary study to address the following questions: (i) to what extent does variation in short-term assimilate supply affect SR among different ecosystems? (ii) what is the contribution of RR to SR across different ecosystems?

MATERIALS AND METHODS

Site description

The study area was situated at the Saihanba Forestry Center in Hebei Province, northern China (117°12′–117°30′ E, 42°10′–42°50′ N, 1400 m a.s.l.). The climate is semi-arid and semi-humid, with a long, cold winter (November to March), and a short spring and summer. Annual mean air temperature and precipitation over the period from 1964 to 2004 were -1.4 °C and 450.1 mm, respectively. The soils are predominantly sandy. Our study site lay within a typical forest-steppe ecotone in a temperate area of northern China. Primary forests were harvested via large-scale industrial logging in the late 1900s and have been replaced by secondary forests and plantations. This site contains the largest area of plantation forests in China, with dominant species of Pinus sylvestris var. mongolica L. (Mongolia pine) and Larix gmelinii var. principis-rupprechtii (Mayr) Pilger (Prince Rupprecht's larch). The secondary forest mainly consists of Betula platyphylla Sukacz. (birch). The detailed for the study area were described by W. Wang et al (2010a).

Clipping experiment

Typical meadow grassland dominated by *Leymus* chinensis (Trin.) Tzvel. was selected to conduct a clipping experiment at the peaks of standing biomass (August 2008). Three areas of 10×10 m for each plot were clipped to a height 2 cm, whist three remained unclipped. Immediately before the clipping treatment

both control and clipped plots were measured for soil and root respiration to obtain a reference value. SR was measured using an LI-8100 soil CO₂ flux system. In each plot, five polyvinyl chloride (PVC) collars (10 cm inside diameter, 6 cm height) were inserted 3 cm into the soil, and were left in the same locations throughout the study. The five PVC collars were placed in the central part of each plot, one in each of the four corners, and the fifth in the middle. Living plants inside the collars were clipped at the soil surface 1 day before each measurement. Soil temperature was recorded during respiration measurements near each collar at 5 cm soil depth with a LI-COR 8100 temperature probe. Soil water content (percent volumetric) at a depth of 10 cm was measured using time domain reflectometry (Soil moisture Equipment Corp., Santa Barbara, California).

Mass specific root respiration (R_m) was measured on excised roots at 0–30 cm soil depth from 4–6 random locations per plot using 5 cm diameter soil cores. Soil cores were transported to a nearby laboratory (less than 30 min travel time per site), and then the cores from each plot were composited. Roots were washed from soil cores with water over a 1.3 mm mesh size screen. We measured R_m by determining the increase of CO₂ concentration with the time at a standard temperature (20 ± 0.4 °C) and atmospheric CO₂ concentration (366 ± 13 µmol mol⁻¹) (Bahn et al. 2006) using the chamber attached to a Li-8100 soil CO₂ Flux system (LI-COR Inc., Lincoln, NE, USA). The details about the measurement protocol were described by W. Wang et al (2010b).

Trenching experiments

During the growing season of 2008, we selected 15 independent forest plots arranged as three replicates for each age classes in Mongolia pine (~15, ~25, and ~35 years) and Prince Rupprecht's larch plantations (~15 and ~35 years). Trenching is a common method to determine *in situ* RR to insert root exclusion to sever roots and then to measure soil carbon dioxide efflux in and outside the exclusion. We used relatively small

root exclusions (SRE) (10 cm diameter plastic pipe) with 70 cm long, installed and measured within a growing season. Within 1–3 weeks, the SREs was reported to provide similar RR estimates to those made with long-used, large root exclusions (2.5 x 3.0 m) (LREs) that had been in place for nearly 10 months (Vogel and Valentine, 2005). The measurements of soil CO₂ efflux above these PVC tubes began immediately after installation to examine the transient response of dead root decomposition. The measurement of SR, soil temperature and soil water content were conducted using the same methods described above.

RESULTS AND DISCUSSIONS

Effect of assimilate supply on SR in a meadow grassland

SR significantly reduced by 25, 35 and 49 % when 4, 6 and 16 days after clipping (Fig. 1, a) in a meadow grassland dominated by *Leymus chinensis*. No significant change occurred for soil temperature and soil water content (Fig. 1, b, c). Clipping reduced significantly mass specific respiration of fine roots (Fig. 1, d). Our results suggest that SR and its root-derived component showed a strong response to the changes of short-term assimilate supply. Our conclusion was consistent with the results of S. Wan and Y. Luo (2003), who showed that clipping significantly reduced SR, independent of the changes of physical environment (soil temperature or moisture). The similar response was also observed in a Kansas steppe (Bremer et al., 1998) and in a Minnestota steppe (Craine et al., 1999). However, in a meadow site, RR was reported to be little affected by clipping for the duration of 8–14 days (Bahn et al., 2006). The possible reason may be attributable to the assumption that RR was largely maintained by carbohydrate reserves (Chapin et al., 1990; Pregitzer et al., 2000; Hugberg et al., 2001; Bazot et al., 2005). The discrepancies suggest that there exists a great variation in the responses of SR and its root-derived components to short-term assimilate supply among different species.



Fig. 1. Effects of clipping on soil respiration (a), soil temperature at 5 cm soil depth (b), soil water content at 10 cm soil depth (c) and mass specific respiration of fine roots (< 2 mm diameter) (d) in a meadow grassland of a forest-steppe ecotone, northern China. Values are mean ± S.D.

Effects of assimilate supply on SR across different forest types

In our study, we used deep small soil collars to cuts off the supply of aboveground photosynthate to roots, instead of traditional trenching method to partition soil CO₂ efflux. This method has been proved to be a useful technique to estimate relative contribution of heterotrophic respiration and autotrophic respiration (Buchmann, 2000; Zhou et al., 2007). The merits and shortcoming of this method were described by X. Zhou et al. (2007). In this study, we found that SR from trenched plots was initially higher than that from untrenched plot for all the forest types (Fig. 2). After a specific period of time, SR began to decline in the trenched plots. In the 12-year-old Mongolia pine and 12-year-old Prince Rupprecht's larch, it took approximately 45 days for the dissipation of the transient CO₂ flush, whereas it took roughly 60 days in 23-years and 39-years old Mongolia pines and 42-year-old Prince Rupprecht's larch. Our results were similar with previous results (Lee et al., 2003; Wang, Yang, 2007; Zhou et al., 2007). The observed higher respiration rate soon after trenching may be connected with the disturbance of soil from excising roots (Uchida et al., 1998), increased substrate supply for microbial respiration (Ohashi et al., 2000) and quick-decomposition of fine-roots and their associated fungal hyphae severed by trenching (Ewel et al., 1987; Rey et al., 2002; Lee et al., 2003).

We estimated RR by the difference of respiration rates between control plot and trenching one when a significant lower respiration rate was observed in the trenched plots. The contribution of RR to SR ranged from 10–40 % (Fig. 3), with higher values in 13 years old Prince Rupprecht's larch.

This work was supported by the National Natural Science Foundation of China (Project Nos. 30870408 and 30670342).



Fig. 2. Comparison of soil respiration between trenching plot and control one among different forest types including 12-, 23-, and 39-year-old Pinus sylvestris (a, b, c), 12-, and 42-year old Larix gmelinii var. principis-rupprechtii (d, e). Values are means ± S.D.



Fig. 3. Contribution of root respiration to soil respiration among different forest types. P1, P2, P3 are 12-, 23-, and 39-year-old *Pinus sylvestris*; L1, L2 are 25- and 42-year old *Larix gmelinii* var. *principis-rupprechtii*. Values are means ± S.D.

REFERENCES

- Andrews J.A., Harrison K.G., Matamala R., Schlesinger W.H. Separation of root respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE) // Soil Sci. Soc. Am. J. 1999. Vol. 63. № 5. P. 1429–1435.
- Baggs E.M. Partitioning the components of soil respiration: a research challenge // Plant Soil. 2006. Vol. 284. № 1–2. P. 1–5.
- Bahn M., Knapp M., Garajova Z., Pfahringer N., Cernusca A. Root respiration in temperate mountain grasslands differing in land use // Global Change Biol. 2006. Vol. 12. Nº 6. P. 995–1006.
- Bazot S., Mikola J., Nguyen C et al. Defoliation-induced changes in carbon allocation and root soluble carbon concentration in fieldgrown *Lolium perenne* plants: do they affect carbon availability, microbes and animal tropic groups in the soil? // Funct. Ecol. 2005. Vol. 19. № 5. P. 886–896.
- Bhupinderpal-Singh Nordgren A., Ottosson Löfvenius M., Högberg M.N., Mellander P.-E., Högberg P. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year// Soil Biol. Biochem. 2003. Vol. 27. № 8. P. 753–760.
- Binkley D., Stape J.L., Takahashi E.N., Ryan M.G. Tree-girdling to separate root and heterotrophic respiration in two Eucalyptus stands in Brazil // Oecologia. 2006. Vol. 148. № 3. P. 447–454.
- Bond-Lamberty B., Thomon, A. A global database of soil respiration data // Biogeosci. Discuss. 2010. Vol. 7. № 1. P. 1321–1344.
- Bond-Lamberty B., Wang C.K., Gower S.T. A global relationship between the heterotrophic and autotrophic components of soil respiration// Global Change Biol. 2004. Vol. 10. № 10. P. 1756–1766.
- Boone R.D., Nadelhoffer K.J., Canary J.D., Kaye J.P. Roots exert a strong influence on the temperature sensitivity of soil respiration // Nature. 1998. Vol. 396. № 6711. P. 570–572.
- Bremer D.J., Ham J.M., Owensby C.E. et al. Responses of soil respiration to clipping and grazing in a tallgrass prairie // J. Environ. Quality. 1998. Vol. 27. № 6. P. 1539–1548.
- Buchmann N. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands // Soil Biol. Biochem. 2000. Vol. 32. № 11–12. P. 1625–1635.
- Chapin F.S.III., Schulze E.D., Mooney H.A. The ecology and economics of storage in plants // Ann. Rev. Ecol. System. 1990. Vol. 21. P. 423–447.
- Craine J.M., Wedin D.A., Chapin F.S.III. Predominance of ecophysiological controls on soil CO₂ flux in a Minnesota grassland // Plant Soil. 1999. Vol. 207. № 1. P. 77–86.
- Ekblad A., Högberg P. Natural abundance of C-13 in CO₂ respired from forest soils reveals speed of link between tree photosynthesis and root respiration // Oecologia. 2001. Vol. 127. № 3. P. 305–308.

- Grace J. Understanding and managing the global carbon cycle // J. Ecol. 2004. Vol. 92. № 2. P. 189–202.
- Hanson P.J., Edwards N.T., Garten C.T., Andrews J.A. Separating root and soil microbial contributions to soil respiration: a review of methods and observations // Biogeochem. 2000. Vol. 48. № 1. P. 115–146.
- Högberg P., Nordgren A., Buchmann N., Taylor A.F.S., Ekblad A., Hogberg M.N., Nyberg G., Ottosson-Lofvenius M., Read D.J. Large-scale forest girdling shows that current photosynthesis drives soil respiration // Nature. 2001. Vol. 411. № 6839. P. 789–792.
- Högberg P., Singh B., Löfvenius M.O., Nordgren A. Partitioning of soil respiration into its autotrophic and heterotrophic components by means of tree-girdling in old boreal spruce forest // Forest Ecol. Manag. 2009. Vol. 257. № 8. P. 1764–1767.
- Högberg P., Nordgren A., Buchmann N., Taylor A.F.S., Ekblad A., Hogberg M.N., Nyberg G., Ottosson-Lofvenius M., Read D.J. Large-scale forest girdling shows that current photosynthesis drives soil respiration // Nature. 2001. Vol. 411. № 6839. P. 789–792.
- Högberg P., Read D.J. Towards a more plant physiological perspective on soil ecology // Trends Ecol. Evol. 2006. Vol. 21. № 10. P. 548–554.
- Janssens I.A., Lankreijer H., Matteucci G. et al. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests // Global Change Biol. 2001. Vol. 7. № 3. P. 269–278.
- Kuzyakov Y. Sources of CO₂ efflux from soil and review of partitioning methods // Soil Biol. Biochem. 2006. Vol. 38. № 3. P. 425–448.
- Kuzyakov Y., Cheng W. Photosynthesis controls of rhizosphere respiration and organic matter decomposition // Soil Biol. Biochem. 2001. Vol. 33. № 14. P. 1915–1925.
- Lee M.S., Mo W.H., Koizumi H. Soil respiration of forest ecosystems in Japan and global implications // Ecol. Res. 2006. Vol. 21. № 6. P. 828–839.
- Lee M.S., Nakane K., Nakatsubo T., Koizumi H. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest // Plant Soil. 2003. Vol. 255. № 1. P. 311–318.
- Luo Y.Q., Jackson R.B., Field C.B. Elevated CO₂ increases belowground respiration in California grasslands // Oecologia. 1996. Vol. 108. № 1. 130–137.
- Marsden C., Nouvellon Y., Bou A.T.M., Saint-Andre L., Jourdan C., Kinana A., Epron D. Two independent estimations of stand-level root respiration on clonal Eucalyptus stands in Congo: up scaling

of direct measurements on roots versus the trenched-plot technique // New Phytol. 2008. Vol. 177. Nº 3. P. 676–687.

- Moyano F.E., Kutsch W.L., Rebmann C. Soil respiration fluxes in relation to photosynthetic activity in broad-leaf and needle-leaf forest stands // Agri. For. Meteor. 2008. Vol. 148. № 1. P. 135–143.
- Ohashi M., Gyokusen K., Saito A. Contribution of root respiration to total soil respiration in a Japanese cedar (*Cryptomeria japonica* D. Don) artificial forest // Ecol. Res. 2000. Vol. 15. № 3. P. 323–333.
- Pregitzer K.S., King J.S., Burton A.J. et al. Responses of tree fine roots to temperature // New Phytol. 2000. Vol. 147. № 1. P. 105–115.
- Raich J.W., Tufekcioglu A. Vegetation and soil respiration: correlations and controls // Biogeochem. 2000. Vol. 48. № 1. P. 71–90.
- Raich J.W., Schlesinger W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate // Tellus. Vol. 44B. № 2. P. 81–99.
- Rey A., Pegoraro E., Tedeschi V. et al. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy // Global Change Biol. 2002. Vol. 8. № 9. P. 851–866.
- Rustad L.E., Huntington T.G., Boone R.D. Controls on soil respiration: implications for climate change // Biogeochem. 2000. Vol. 48. № 1. P. 1–6.
- Subke J.A., Inglima I., Cotrufo F. Trends and methodological impacts in soil CO₂ efflux partitioning: A metaanalytical review // Global Change Biol. 2006. Vol. 12. № 6. P. 921–943.
- Uchida M., Nakatsubo T., Horikoshi T., Nakane K. Contribution of micro-organisms to the carbon dynamics in black spruce (*Picea mariana*) forest soil in Canada // Ecol. Res. 1998. Vol. 13. № 1. P. 17–26.

- Vogel J.G., Valentine D.W. Small root exclusion collars provide reasonable estimates of root respiration when measured during the growing season of installation // Can. J. For. Res. 2005. Vol. 35. № 9. P. 2112–2117.
- Wan S.Q., Luo Y.Q. Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment // Global Biogeochem. Cyc. 2003. Vol. 17. № 2. P. 1054.
- Wang C.K, Yang J.Y., Zhang Q.Z. Soil respiration in six temperate forests in China// Global Change Biol. 2006. Vol. 12. № 11. P. 1–12.
- Wang C.K., Yang J.Y. Rhizospheric and heterotrophic components of soil respiration in six Chinese temperate forests // Global Change Biol. 2007. Vol. 13. № 1. P. 123–131.
- Wang W., Fang J.Y. Soil respiration and human effects on global grasslands. Glob. Planetary Change. 2009. Vol. 67. № 1–2. P. 20–28.
- Wang W., Peng S.H., Wang T., Fang J.Y. Winter soil CO₂ efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China // Soil Biol. Biochem. 2010a. Vol. 42. № 3. P. 451–458.
- Wang W., Peng S.H., Fang J.Y. Root respiration and its relation to nutrient contents in soil and root and EVI among 8 ecosystems, northern China // Plant Soil. 2010b. Vol. 333. № 1–2. P. 391–401.
- Zhou X.H., Wan S.Q., Luo Y.Q. Source components and interannual variability of soil CO₂ efflux under experimental warming and clipping in a grassland ecosystem // Global Change Biol. 2007. Vol. 13. № 4. P. 761–755.