Front. For. China 2008, 3(2): 131–138
DOI 10.1007/s11461-008-0027-6

REVIEW

Yumei ZHOU, Shijie HAN, Junqiang ZHENG, Lihua XIN, Haisen ZHANG

Effects of elevated CO_2 concentrations on soil microbial respiration and root/rhizosphere respiration in forest soils

Abstract The two main components of soil respiration, i.e., root/rhizosphere and microbial respiration, respond differently to elevated atmospheric CO_2 concentrations both in mechanism and sensitivity because they have different substrates derived from plant and soil organic matter, respectively. To model the carbon cycle and predict the carbon source/sink of forest ecosystems, we must first understand the relative contributions of root/rhizosphere and microbial respiration to total soil respiration under elevated CO_2 concentrations. Root/rhizosphere and soil microbial respiration have been shown to increase, decrease and remain unchanged under elevated CO_2 concentrations. A significantly positive relationship between root biomass and root/rhizosphere respiration has been found. Fine roots respond more strongly to elevated CO_2 concentrations than coarse roots. Evidence suggests that soil microbial respiration is highly variable and uncertain under elevated CO_2 concentrations. Microbial biomass and activity are related or unrelated to rates of microbial respiration. Because substrate availability drives microbial metabolism in soils, it is likely that much of the variability in microbial respiration results from differences in the response of root growth to elevated CO_2 concentrations and subsequent changes in substrate production. Biotic and abiotic factors affecting soil respiration were found to affect both root/rhizosphere and microbial respiration.

Keywords elevated CO_2 concentrations, rhizosphere, soil microorganism, soil respiration

Translated from *Journal of Plant Ecology*, 2007, 31(3): 386–393 [译自: 植物生态学报]

Yumei ZHOU, Shijie HAN (✉), Junqiang ZHENG, Haisen ZHANG
Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China
E-mail: hansj@iae.ac.cn

Lihua XIN
College of Land and Environment, Shenyang Agricultural University, Shenyang 110161, China

1 Introduction

Global climate models predict that the atmospheric CO_2 concentration is gradually increasing due to human activities, burning of fossil fuel and changes of land use patterns. The increase of CO_2 concentration will affect the photosynthesis of above-ground plant growth, physiological functions of root systems and the soil carbon cycle (Leakey et al., 2002; Ainsworth et al., 2003; Milchunas et al., 2005; Trueman and Gonzalez-Meler, 2005). As the second largest carbon reservoir, soil is one of the most important sources of atmospheric CO_2 (Jenkinson et al., 1991). The amount of CO_2 emissions from the soil, in terms of C, is about 77×10^{15} g/year (Raich and Potter, 1995). The uptake and loss of carbon remained in balance before there was too much human intervention with the environment, especially the disruption of soil. In recent years, CO_2 emission from the soil has exceeded the net primary production (NPP) and litter because of increased anthropogenic activities. Therefore, soil respiration plays an important role in the rise of atmospheric CO_2 concentrations (Schlesinger and Andrews, 2000). Forest is the main part of terrestrial ecosystems and contains 46% carbon of the global carbon sink (Dixon et al., 1994). Janssens et al. (2001) estimated that the relative contribution of annual CO_2 emission from forest ecosystems to total ecosystem respiration was 69% which highlights the importance of soil respiration in the carbon budgets of forest ecosystems.

Increasing atmospheric CO_2 concentrations directly or indirectly affect the main components of soil respiration, root respiration and microbial respiration by changing the physiological function of root systems and soil carbon dynamics. Root respiration and microbial respiration respond differently in mechanism and sensitivity to elevated CO_2 concentrations. If we are to establish a carbon cycle model, evaluate carbon source/sink relationships and monitor soil intervention, we must first understand the relative contributions of root respiration and respiration by soil heterotrophy to total soil respiration and their response patterns to elevated CO_2 concentrations.

Many papers have been published on forest soil respiration at ambient and elevated CO_2 concentrations, but research on the relative contribution of root respiration and microbial respiration to total soil respiration is still rare, especially under elevated CO_2 concentrations. A few studies on separating root or microbial respiration from total soil respiration are limited to northeastern districts of China (Jiang et al., 2004; Liu et al., 2005; Zhang et al., 2005). Research findings in this field are necessary to evaluate carbon budgets of forest ecosystems against the background of global change.

2 Methods of separating root/rhizosphere respiration or microbial respiration from total soil respiration

2.1 Definition of root/rhizosphere respiration and microbial respiration

The efflux of CO_2 from forest soils is a combination of the activity of autotrophic roots and associated rhizosphere organisms, heterotrophic bacteria and fungi active in the organic and mineral soil horizons and soil faunal activities (Edwards et al., 1970). The CO_2 emission from soil faunal and non-biological processes is often ignored because it only accounts for a small proportion of total emission (Sing and Gupta, 1977). In field measurements, soil respiration mainly refers to root respiration and microbial respiration. In fact, root respiration is part of autotrophic respiration while microbial respiration is a form of heterotrophic respiration. At present, there are still no methods to differentiate microbial respiration, whose substrate is root exudation, from root respiration (Hanson et al., 2000).

Root respiration and respiration by soil organisms utilize C derived from plants or organic soil matter, respectively (Susfalk et al., 2002). Root respiration was defined by Wiant (1967) to include all processes occurring in the rhizosphere. Wiant (1967) stated that root respiration included all respiration of living root tissues, the respiration of symbiotic mycorrhizal fungi and associated microorganisms and the decomposing organisms operating on root exudates and recent dead root tissues in the rhizosphere. Live root respiration can be divided into coarse and fine root respiration, or growth and maintenance respiration according to composition or function (Amthor, 2004; Yang et al., 2004). The fraction of soil respiration derived from live roots is independent on soil C pools and contributions of live root to total soil respiration can be used to infer rates of long term soil C storage (Hanson et al., 2000). Roots respire plant photosynthates newly produced by the canopy (Högberg et al., 2001). Alternatively, microbial decomposition can affect the C balance of the ecosystem by releasing CO_2 from soil organic matter that ranges in age from the most recent (e.g. fine-root turnover) to years and even millennia (e.g. litter and humified soil C) (Trumbore, 2000). With further research on global change, the contribution of the root/rhizosphere respiration or microbial respiration needs to be understood to establish a process model and to evaluate implications of environmental factors on soil carbon cycles and carbon sequestration.

2.2 Methods of partitioning soil respiration: advantages and disadvantages

The method of measuring root/rhizosphere respiration and microbial respiration can be simply divided into component integration, root exclusion, isotopic methods (Hanson et al., 2000) and root biomass extrapolation (Li et al., 2002). These methods may overestimate or underestimate the values of soil respiration in the field by disturbing the soil surface equilibrium during measuring.

The main disadvantage of the component integration approach is that it causes considerable destruction of the *in situ* status of the soil. The method is suitable only when the integration of the component parts equals the total soil respiration. Therefore, this method is often of limited value in the field. Root exclusion methods include root removal, trenching and gap analysis. Rhizosphere respiration and microbial respiration are indirectly estimated by measuring soil respiration with and without roots. The advantages of root removal are that roots may be removed completely and that, at the same time, the root morphology and biomass can be measured. The disadvantage is that disturbance of the soil is considerable. Compared with the root removal approach, trenching greatly reduces the disturbance of soil. Because of the effect of residual decomposing roots left in the trenched plots, the soil respiration of trenched plots should be measured several months later. In addition, the microenvironment of areas with roots is different from that without roots after roots are clipped for a period of time, which can result in a biased estimation. The gap method demands that measurement must be conducted in a large stand to cover different forest types. The disadvantages of the gap method are that the physical and chemical properties in soils vary at different plots. Among these methods, the isotopic method is almost perfect because it may avoid disturbing the soil. But the obvious disadvantages of this method are the complex of measurement procedures, the difficulties encountered and its cost. Nor is it suitable to measure many plots at the same time in the field. The isotopic approach is not suitable for the partition soil respiration in free-air CO_2 enrichment (FACE) and in open-top chambers with elevated CO_2 concentrations, although it has been applied in several investigations (Andrews et al., 1999; Lin et al., 1999, 2001). Root respiration rates will be overestimated when elevated CO_2 exposure exceeds one year because soil organic matter contains some exotically labeled carbon. Carbon

from root respiration and soil organic matter cannot be differentiated. The method of root biomass extrapolation is based on correlation between root biomass and soil respiration rates. This method demands a large number of replications and a root biomass gradient.

3 Effects of elevated CO_2 concentrations on root/rhizosphere respiration and microbial respiration

Root respiration and microbial respiration respond differently to high CO_2 concentrations. Rhizosphere respiration has been reported to be the most responsive to elevated CO_2 (Lin et al., 2001). Elevated CO_2 concentrations affect root growth, the amount of root exudation and the accumulation of soil carbon, which will cause further changes in root respiration and microbial respiration. There is a significant, positive relationship between root biomass and root respiration (Pregitzer et al., 2000). The increase of microbial respiration is closely related to the enhancement of the amount of root exudation and above-ground litter (Insam et al., 1999; Zak et al., 2000). If the growth rate of roots exceeds that of the aboveground part, the release of CO_2 from the rhizosphere may exceed the assimilation of CO_2, which will result in a continuous rise of atmospheric CO_2. Therefore, reducing rhizosphere respiration has the same effect as higher soil carbon stock to balance atmospheric CO_2 concentration.

3.1 Effects of elevated CO_2 concentrations on root/rhizosphere respiration

Root/rhizosphere respiration is stimulated or decreased under elevated CO_2 concentrations (Table 1). The root respiration of *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris* decreased significantly compared with that at ambient CO_2, after they had grown at open top chambers with exposure for 20 months to 700 μmol/mol CO_2. However, the amount of soluble sugar of roots increased considerably (Crookshanks et al., 1998). The amount of starch in roots declined for *Fraxinus excelsior* and *Quercus petraea*, but increased for *Pinus sylvestris*. Fine root respiration contributed 30% to 70% of the total soil respiration. Fine root respiration provides energy for protein turnover, maintenance of an ion gradient, production of new tissue and assimilation of nutrition (Raich and Schlesinger, 1992). Annual fine root respiration of *Pinus taeda*, growing at 560 μmol/mol CO_2 in Duke Forest and Oak Ridge National Laboratory, decreased by 17% (George et al., 2003). Root specific maintenance respiration for *Pinus taeda* contributed 92% to total soil respiration, while growth respiration and nitrogen uptake respiration formed only small components of maintenance respiration. Total fine root respiration decreased, although growth respiration increased by 37% because maintenance respiration decreased by 17%.

Three-year-old *Pinus sylvestris* seedlings were planted in open top chambers located on the campus of the University of Antwerp. After six months exposure to 700 μmol/mol CO_2, the respiration of detached roots increased by 46%. Rhizosphere respiration *in situ* was also enhanced and accounted for 66% to 71% of total soil respiration under elevated CO_2 concentrations and for 50% to 57% of ambient CO_2. In addition, root length and biomass, root production, carbon and the amount of nitrogen also increased at elevated CO_2 concentrations (Janssens et al., 1998). Hence, carbon dioxide efflux from root/rhizosphere at elevated CO_2 concentrations significantly increased, primarily, due to large enhancements in root biomass and production (Griffin et al., 1997; Andrews et al., 1999; Lin et al., 2001). There is also a significant, positive relationship between root biomass and root respiration (Pregitzer et al., 2000).

The increase of total soil respiration in 20-year-old *Pinus sylvestris* growing at 700 μmol/mol CO_2 in the boreal zone of Finland was primarily due to the higher root/rhizosphere respiration rather than microbial decomposition of above-ground litter. The stimulation of root/rhizosphere respiration was closely related to fine root biomass. Needle area was found to be an important predictor of soil respiration, particularly during the months of high root growth, thus supporting the assumption of a close link between photosynthesis and soil CO_2 efflux (Niinistö et al., 2004). Elevated CO_2 concentrations promote the growth and biomass of fine roots and at the same time can speed up carbon transfer from dead fine roots (Tingey et al., 1997). Both are related to the increase of rhizosphere respiration. In addition, the increase of coarse roots biomass can also stimulate soil respiration (Vose et al., 1995; Edwards and Norby, 1999).

The direction and magnitude of response of root/rhizosphere respiration to elevated CO_2 concentrations is related to the duration of exposure, availability of soil resources (e.g. the amount of nitrogen) and expression method (Griffin et al., 1997; Ball et al., 2000; Tingey et al., 2000). Tingey et al. (2000) argued that it is not clear whether the increase of fine root growth can be maintained for a long time on exposure to elevated CO_2 concentrations. The model by Lin et al. (2001) predicts that the initial increase of root growth may decrease with CO_2 treatment because the nutritional status of soil cannot afford a gradually improved photosynthesis. Root/rhizosphere respiration is directly affected by soil nutrition availability, especially the amount of nitrogen. For *Pinus taeda* and *Pinus ponderosa*, increasing N availability generally leads to higher respiration. Root N concentration is significantly correlated with root respiration, such that seedlings with higher root N concentrations had higher rates of specific root respiration (Griffin et al., 1997).

Table 1 Soil microbial respiration and root/rhizosphere respiration under elevated CO_2 concentrations

species	soil characteristics	CO_2 concentration/ $\mu mol \cdot mol^{-1}$	length of exposure	root/rhizosphere respiration	microbial respiration	Experimental method	experimental facilities	reference
Fraxinus excelsior	podsol	700	20 months	decrease		incubation	OTC	Crookshanks et al., 1998
Quercus petraea	podsol	700	20 months	decrease		incubation	OTC	Crookshanks et al., 1998
Pinus sylvestris	podsol	700	20 months	decrease		incubation	OTC	Crookshanks et al., 1998
Pinus taeda	alfisol	+200	four years	decrease		detached measurement	FACE	George et al., 2003
Pinus taeda	alfisol	+200	one year	increase		carbon isotope tracer	FACE	Andrews et al., 1999
Pinus taeda	sterilized river sand	700[1]	five months	increase		incubation	greenhouse in phytotron	Griffin et al., 1997
Pinus ponderosa	sterilized river sand	700	five months	increase	decrease	incubation	greenhouse in phytotron	Griffin et al., 1997
Pinus sylvestris	sandy forest soil	700	six months	increase		detached measurement	OTC	Janssens et al. 1998
Pinus sylvestris	sandy forest soil	700	six months	increase		excised roots	OTC	Janssens et al. 1998
Populus tremuloides; *Betula papyrifera*; *Acer saccharum*	sandy loam	560	three years		increase	carbon isotope	FACE	Phillips et al. 2002
seven tropical C_3 plants	forest soil	610	530 days		increase	substrate induction	greenhouse	Insam et al. 1999
Liquidambar styraciflua	aquic hapludult	+200	two years	increase		detached measurement	FACE	George et al., 2003
Pseudotsuga menziesii	forest soil	+200	two years	increase	decrease	dual stable isotope	controlled-environment chamber	Lin et al., 2001
Acer saccharum	silt loam	+300	three years	increase	no significant change	root-exclusion	OTC	Edwards and Norby, 1999
Acer rubrum	silt loam	+300	three years	increase	no significant change	root-exclusion	OTC	Edwards and Norby, 1999
Lindera benzoin	sandy loam	700	six growing seasons	increase/ no change	increase	detached measurement	enclosed octagonal chamber	Ball et al., 2000

Note: OTC means open-top chamber, FACE means free-air CO_2 enrichment

Various plants respond differently to elevated CO_2 concentrations. Annual fine root respiration of *Pinus taeda* decreased by 17% and that of *Liquidambar styraciflua* increased by 86%, although both tree species grew at similar CO_2 concentrations (George et al., 2003). The root respiration rate of *Pinus taeda* and *Pinus ponderosa* was similar at ambient CO_2, but the former was significantly higher than the latter when measured at 700 μmol/mol CO_2 (Griffin et al., 1997). The root biomass of *Lindera benzoin* significantly increased after exposure to 700 μmol/mol CO_2 for six growing seasons. When respiration was expressed per unit of dried weight of roots, no significant difference was observed between the ambient and elevated CO_2 systems. However, when these values were expressed in terms of per unit of soil, a significant increase was observed in root respiration in samples from field chambers exposed to elevated CO_2 concentrations. This resulted from a 30% increase in the dry weight of roots present in field chambers exposed to elevated CO_2 concentrations (Ball et al. 2000).

3.2 Effects of elevated CO_2 on microbial respiration

Since the CO_2 concentration in the soil is already significantly higher than in the atmosphere, it is unlikely that increasing atmospheric CO_2 will directly affect rhizosphere microflora. On the other hand, the increase of total rhizodeposition and the change of composition of rhizosphere-released material will have the potential to alter the microbial community structure and the activities of rhizosphere microorganisms (Schortemeyer et al., 1996). Soil carbon from root exudation or dead root tissues will change after exposure to elevated CO_2 concentrations, i.e., the carbon source or energy for microbial decomposition will change. Microbial respiration in forest soils may increase, decrease or show no significant change under elevated CO_2 concentrations (Zak et al., 1993; Johnson et al., 1994; Ball et al., 2000; Lin et al., 2001). Elevated CO_2 concentrations generally increase root exudation and below-ground carbon distributions (Cheng 1999; Wiliams et al. 2000), which can stimulate soil microbial respiration. Soil microbial respiration of *Lindera benzoin* per unit area increased after exposure to 700 μmol/mol CO_2 for six growing seasons (Ball et al., 2000). However, it did not change significantly for *Pinus ponderosa* (Johnson et al., 1994). Of course, soil microbial respiration shows a decrease in some studies under elevated CO_2 concentrations. Soil microorganisms prefer easily decomposable root-derived material (Schortemeyer et al., 1996). The increased allocation of labile C to soil can serve as a substrate for microbes, thus reducing the reliance of microbial respiration on C from soil organic matter which, as a consequence, leads to reduced organic soil matter oxidation (Cheng, 1999; Lin et al., 2001).

In fact, rhizosphere respiration measured in the field includes part of microbial decomposition of root exudation. Therefore, it is very complicated to estimate accurately the contribution of microbial respiration to total soil respiration. One reason is that the effect of elevated CO_2 levels on soil microbial respiration is indirect. Another major reason is that there are many potential uncertainties, deriving from many dynamic factors, such as CO_2 exposure duration, the status of the ingrowth of roots, amount of root exudation and stage of root development. Soil microbial parameters include the number of microbes, microbial biomass, microbial activity, specific microbial population etc. (Sadowsky and Schortemeyer, 1997). The changes of these parameters may or may not be related to microbial respiration.

The microbial respiration of *Populus tremuloides*, *Betula papyrifera* and *Acer saccharum* increased by 29% after exposure to 560 μmol/mol CO_2 for a period of three years. There is no significant difference in microbial respiration among tree species. Elevated CO_2 concentrations changed microbial community structures and increased microbial activity but did not affect microbial biomass (Phillips et al., 2002). Zak et al. (2003) also reported similar results during their investigation of nutrition cycles in FACE. The microbial respiration of seven tropical plants (*Elettaria cardamomum*, *Ficus benjamina*, *F. Pumila*, *Heliconia humilis*, *Ctenanthe lubbersiana*, *Cecropia peltata* and *Epipremnum pinnatum*) increased by 19% after a 530-day exposure to 610 μmol/mol CO_2, but microbial biomass did not show significant changes, although the number of bacteria and the microbial biomass C/N ratio increased significantly (Insam et al., 1999). In their summary Zak et al. (2000) concluded that the relative change in microbial biomass below woody plants ranged from a 52% decline to a 121% increase, whereas the extent to which microbial respiration was stimulated under elevated CO_2 levels ranged from a 4% decline to a 72% increase. There is no significant relationship between microbial biomass and microbial respiration, although microbial biomass is the most active and labile ingredient in soils. The uncertainty of microbial respiration is largely the result of the difference in response of plants to elevated CO_2 concentrations and their litters.

4 Factors affecting soil respiration

The response of root/rhizosphere respiration to various environmental factors is different from that of microbial respiration. Among these, soil temperature is a major factor to affect the root/rhizosphere respiration. Respiration of fine roots is more temperature sensitive than that of coarse roots (Widén and Majdi, 2001). Also, evidence of a clear seasonal trend of root/rhizosphere respiration and total soil respiration suggests a significant effect of soil temperature on root/rhizosphere respiration (Edwards

and Norby, 1999; Lin et al., 1999; Widén and Majdi, 2001; Jiang et al., 2005). Elevated CO_2 concentrations must cause an increase in temperature. In most simulated experiments without temperature control, the increase in magnitude of air temperature is not consistent. It is still very difficult to quantify the temperature effect caused by elevated CO_2 concentrations in facilities with cooler temperatures. Therefore, we cannot evaluate accurately the effect of temperature on root or microbial respiration in FACE or open top chamber (OTC). Lin et al. (1999) applied a stable isotopic approach to investigate the impact of elevated CO_2 concentrations (+200 μmol/mol CO_2) and increased temperature (+4°C) on different components of soil respiration in Douglas-fir. The oxidation of soil organic matter was only stimulated by increasing temperature. Release of newly fixed carbon as root respiration was the most responsive to elevated CO_2 concentrations. Both elevated CO_2 concentrations and increased temperature stimulated rhizosphere respiration.

Soil water is another important factor affecting root/rhizosphere respiration and microbial respiration. Elevated CO_2 concentrations decrease transpiration of the canopy and increase the efficiency of water use by plants, which indirectly decreases soil water stress and increases carbon input as metabolic substrates of microbe (Owensby et al., 1993; Field et al., 1995). Rice et al. (1994) reported that soil microbial activity was strongly correlated with the amount of soil water under elevated CO_2 concentrations. At present no special studies on the effects of soil moisture on root/rhizosphere respiration and microbial respiration under elevated CO_2 concentrations are in progress. The changes in physiological and biochemical functions of above-ground parts will affect water absorption and utilization of root systems. The changes in the amount of soil water will further lead to changes in species and amounts of microorganisms. Therefore, soil water can indirectly affect root/rhizosphere respiration or microbial respiration. The response pattern of root/rhizosphere respiration and microbial respiration to soil water is not clear.

There are many other environmental factors affecting soil respiration and its components. Relatively high CO_2 concentrations in the soil/atmosphere interface affect soil respiration by changing the diffusion rate of CO_2 from soil to atmosphere (Zhou et al., 2006). Length of CO_2 exposure is also an important factor, potentially affecting root/rhizosphere respiration and microbial respiration. Recent studies have shown an initial increased effect with CO_2 treatment on soil respiration (Thomas et al., 2000; Niinistö et al., 2004). To date, most studies, reporting stimulation of soil respiration under elevated CO_2 concentrations have been of relatively short duration, less than three years. Much longer observation periods are necessary to determine if initial responses to elevated CO_2 decline (King et al., 2004).

5 Suggestions

1) The dynamic response process of root systems to elevated CO_2 concentrations directly affects substrates of microbial decomposition and microbial activity so that long-term research is essential.

2) The response mechanism of root/rhizosphere respiration and microbial respiration to elevated CO_2 concentrations is still not clear. Future investigations should emphasize the interaction of soil enzymes closely related to soil respiration, structure and function of microbial communities, root morphology and nutritional dynamics.

3) Photosynthesis of the canopy will directly or indirectly affect root/rhizosphere respiration and microbial respiration with a long-term exposure to elevated CO_2 concentrations. Therefore, the carbon input from above-ground part should be considered when partitioning the contribution of root/rhizosphere and microbial respiration to total soil respiration.

Acknowledgements This study was supported by the National Natural Science Foundation of China (Grant No. 30400051), the key project of the National Natural Science Foundation of China (Grant No. 90411020) and the Knowledge Innovation Program of CAS (No. KZCX2-YW-416).

References

Ainsworth E A, Davey P A, Hymus G J, Osborne C P, Rogers A, Blum H, Nösberger J, Long S P (2003). Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with *Lolium perenne* grown for 10 years at two nitrogen fertilization levels under Free Air CO_2 Enrichment (FACE). Plant Cell Environ, 26: 705–714

Amthor J S (2000). The McCree-de Wit-Penning de Vries-Thomley respiration paradigms: 30 years later. Ann Bot, 86: 1–20

Andrews J A, Harrison K G, Matamala R, Schlesinger W H (1999). Separation of root respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). Soil Sci Soc Am J, 63: 1429–1435

Ball A S, Milne E, Drake B G (2000). Elevated atmospheric-carbon dioxide concentration increases soil respiration in a mid-successional lowland forest. Soil Biol Biochem. 32: 721–723

Cheng W X (1999). Rhizosphere feedbacks in elevated CO_2. Tree Physiol, 19: 313–320

Crookshanks M, Taylor G, Broadmeadow M (1998). Elevated CO_2 and tree root growth: contrasting responses in *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris*. New Phytol, 138: 241–250

Dixon R K, Brown S, Houghton R A, Solomon A M, Trexler M C, Wisniewski J (1994). Carbon pools and flux of global forest ecosystems. Science, 263: 185–190

Edwards C A, Reichle D E, Crossley D A Jr (1970). The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle D E, ed. Analysis of Temperate Forest Ecosystems. New York: Springer-Verlag, 12–172

Edwards N T, Norby R J (1999). Below-ground respiratory responses of sugar maple and red maple saplings to atmospheric CO_2 enrichment and elevated air temperature. Plant Soil, 206: 85–97

Field C B, Jackson R B, Mooney H A (1995). Stomatal responses to increased CO_2: implications from the plant to the global scale. Plant Cell Environ, 18: 1214–1225

George K, Norby R J, Hamilton J G, DeLucia E H (2003). Fine-root respiration in a loblolly pine and sweetgum forest growing in elevated CO_2. New Phytol, 160: 511–522

Griffin K L, Bashkin M A, Thomas R B, Strain B R (1997). Interactive effects of soil nitrogen and atmospheric carbon dioxide on root/rhizosphere carbon dioxide efflux from loblolly and ponderosa pine seedlings. Plant Soil, 190: 11–18

Hanson P J, Edwards N T, Garten C T, Andrews J A (2000). Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry, 48: 115–146

Högberg P, Nordgren A, Buchman N, Taylor A F S, Ekblad A, Högberg M H, Nyberg G, Ottosson-Löfvenius M, Read D J (2001). Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature, 411: 789–792

Insam H, Bååth E, Berreck M, Frostegård A, Gerzabek M H, Kraft A, Schinner F, Schweiger P, Tschuggnall G (1999). Responses of the soil microbiota to elevated CO_2 in an artificial tropical ecosystem. J Microbiol Methods, 36: 45–54

Janssens I A, Crookshanks M, Taylor G, Ceulemans R. (1998). Elevated atmospheric CO_2 increases fine root production, respiration, rhizosphere respiration and soil CO_2 efflux in Scots pine seedlings. Global Change Biol, 4: 871–878

Janssens I A, Lankreijer H, Matteucci G, Kowalski A S, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grünwald T, Montagnani L, Dore S, Rebmann C, Moors E J, Grelle A, Rannik Ü, Morgenstern K, Oltchev S, Clement R, Gudmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen N O, Vesala T, Granier A, Schulze E D, Lindroth A, Dolman A J, Jarvis P G, Ceulemans R, Valentini R (2001). Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biol, 7: 269–278

Jenkinson D S, Adams D E, Wild A (199l). Model estimates of CO_2 emission from soil in response to global warming. Nature, 351: 304–306

Jiang L F, Shi F C, Wang H T, Zu Y G, Takayoshi K (2004). Root respiration in *Larix gmelinii* plantations in Northeast China. Plant Physiol Commun, 40(1): 27–30 (in Chinese)

Jiang L F, Shi F C, Li B, Luo Y Q, Chen J Q, Chen J K (2005). Separating rhizosphere respiration from total soil respiration in two arch plantations in Northeastern China. Tree Physiol, 25: 1187–1195

Johnson D, Geisinger D, Walker R, Newman J, Vose J, Elliot K, Ball T (1994). Soil pCO_2 soil respiration, and root activity in CO_2-fumigated and nitrogen-fertilized ponderosa pine. Plant Soil, 165: 129–138

King J S, Hanson P J, Bernhardt E, Deangelis P, Norby R J, Pregitzer K S (2004). A multiyear synthesis of soil respiration responses to elevated atmospheric CO_2 from four forest FACE experiments. Global Change Biol, 10: 1027–1042

Leakey A D, Press B M, Scholes C J D, Watling J R (2002). Relative enhancement of photosynthesis and growth at elevated CO_2 is greater under sun flecks than uniform irradiance in a tropical rain forest tree seedling. Plant Cell Environ, 25: 1701–1714

Li L H, Han X G, Wang Q B, Chen Q S, Zhang Y, Yang J, Bai W M, Song S H, Xing X R, Zhang S M (2002). Separating root and soil microbial contributions to total soil respiration in a grazed grassland in the Xilin River basin. Acta Phytoecol Sin, 26: 29–32 (in Chinese)

Lin G H, Ehleringer J R, Rygiewicz P T, Johnson M G, Tingey D T (1999). Elevated CO_2 and temperature impacts on different component of soil CO_2 efflux in Douglas-fir terracosms. Global Change Biol, 5: 157–168

Lin G H, Rygiewicz P T, Ehleringer J R, Johnson M G, Tingey D T (2001). Time-dependent responses of soil CO_2 efflux components to elevated atmospheric [CO_2] and temperature in experimental forest mesocosms. Plant Soil, 229: 259–270

Liu Y, Han S J, Hu Y L, Dai G H. Effects of soil temperature and humidity on soil respiration rate under *Pinus sylvestriformis* forest. Chin J Appl Ecol, 16: 1581–1585 (in Chinese)

Milchunas D G, Morgan J A, Mosier A R, Lecain D R (2005). Root dynamics and demography in shortgrass steppe under elevated CO_2, and comments on minirhizotron methodology. Global Change Biol, 11: 1837–1855

Niinistö S M, Silvola J, Kellomäki S (2004). Soil CO_2 efflux in a boreal pine forest under atmospheric CO_2 enrichment and air warming. Global Change Biol, 10: 1363–1376

Owensby C E, Coyne P I, Ham J M, Auen L M, Knapp A K (1993). Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. Ecol Appl, 3: 644–653

Phillips R L, Zak D R, Holmes W E, White D C (2002). Microbial community composition and function beneath temperate trees exposed to elevated atmospheric CO_2 and O_3. Oecologia, 131: 236–244

Pregitzer K S, Zak D R, Maziasz J, DeForest J, Curtis P S, Lussenhop J (2000). Interactive effects of atmospheric CO_2 and soil-N availability on fine roots of *Populus tremuloides*. Ecol Appl, 10: 18–33

Raich J W, Potter C S (1995). Global patterns of carbon dioxide emissions from soils. Global Biogeochem Cy, 9: 23–36

Raich J W, Schlesinger W H (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus, 44B: 81–99

Rice C W, Garcia F O, Hampton C O, Owensby C E (1994). Soil microbial response in tall grass prairie to elevated CO_2. Plant Soil, 165: 67–74

Sadowsky M J, Schortemeyer M (1997). Soil microbial responses to increased concentrations of atmospheric CO_2. Global Change Biol, 3: 217–224

Schlesinger W H, Andrews J A (2000). Soil respiration and the global carbon cycle. Biogeochemistry, 48: 7–20

Schortemeyer M, Hartwig U A, Hendrey G R, Sadowsky M J (1996). Microbial community changes in the rhizospheres of white clover and perennial ryegrass exposed to free air carbon dioxide enrichment (FACE). Soil Biol Biochem, 28: 1717–1724

Susfalk R B, Cheng W X, Johnson D W, Walker R F, Verburg P, Fu S (2002). Lateral diffusion and atmospheric CO_2 mixing compromise estimates of rhizosphere respiration in a forest soil. Can J For Res, 32: 1005–1015

Thomas S M, Cook F J, Whitehead D, Adams J A (2000). Seasonal soil surface carbon fluxes from the root systems of young *Pinus radiata* trees growing at ambient and elevated CO_2 concentration. Global Change Biol, 6: 393–406

Tingey D T, Phillips D L, Johnson M G (2000). Elevated CO_2 and conifer roots: effect on growth and life span and turnover. New Phytol, 147: 87–103

Tingey D T, Phillips D L, Johnson M G, Johnson D W, Ball J T (1997). Effects of elevated CO_2 and N fertilization on fine root dynamics and fungal growth in seedling *Pinus ponderosa*. Environ Exp Bot, 37: 73–83

Trueman R J, Gonzalez-Meler M A (2005). Accelerated belowground C cycling in a managed agriforest ecosystem exposed to elevated carbon dioxide concentrations. Global Change Biol, 11: 1258–1271

Trumbore S (2000). Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecol Appl, 10: 399–411

Vose J M, Elliott K J, Johnson D W, Walker R F, Johnson M G, Tingey D T (1995). Effects of elevated CO_2 and N fertilization on soil respiration from ponderosa pine (*Pinus ponderosa*) in open-top chambers. Can J For Res, 25: 1243–1251

Wiant H V (1967). Has the contribution of litter decay to forest soil respiration been overestimated? J For, 65: 408–409

Widén B, Majdi H (2001). Soil CO_2 efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. Can J For Res, 31: 786–796

Wiliams M A, Rice C W, Owensby C E (2000). Carbon dynamics and microbial activity in tallgrass prairie exposed to elevated CO_2 for 8 years. Plant Soil, 227: 127–137

Yang Y S, Dong B, Xie J S, Chen G S, Li L, Liu D X, Li Z (2004). A review of tree root respiration: significance and methodologies. Acta Phytoecol Sin, 28: 426–434 (in Chinese)

Zak D R, Holmes W E, Finzi A C, Norby R J, Schlesinger W H (2003). Soil nitrogen cycling under elevated CO_2: a synthesis of forest FACE experiments. Ecol Appl, 13: 1508–1514

Zak D R, Pregitzer K S, Curtis P S, Teeri J A, Fogel R, Randlett D L (1993). Elevated atmospheric CO_2 and feedback between carbon and nitrogen cycles. Plant Soil, 151: 105–117

Zak D R, Pregitzer K S, King J S, Holmes W E (2000). Elevated atmospheric CO_2, fine roots, and the response of soil microorganisms; a review and hypothesis. New Phytol, 147: 201–222

Zhang X Q, Wang W J, Zu Y G, Zhang W L (2005). The difference between different components of soil respiration in several types of forests in Northeastern China. J Northeast For Univ, 33(2): 46–47 (in Chinese)

Zhou Y M, Han S J, Xin L H (2006). Soil respiration of *Pinus koraiensis* and *P. sylvestriformis* trees growing at elevated CO_2 concentration. Chin J Appl Ecol, 17: 1757–1760 (in Chinese)