Estimating heterotrophic and autotrophic soil respiration using small-area trenched plot technique: Theory and practice

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Abstract

The trenching method of root exclusion is generally used to estimate heterotrophic (microbial decomposition) (F_h) and autotrophic (root and associated rhizosphere respiration) (F_a) components of soil respiration (F_0), particularly in forest ecosystems. However, some uncertainties exist on the accuracy and interpretation of the results from such experiments using small-area root exclusion plots. Using field and laboratory measurements as well as simulations using a process-based model of CO_2 production and transport in soil, we show that: (a) CO_2 concentrations at or immediately below the depth of root exclusion in small-area root exclusion plots are similar to those at the same depth in nearby undisturbed soil and (b) the contribution of soil CO_2 flux from below the root exclusion depth to the measured efflux at the surface of a root exclusion plot (F_{0re}) is increased because of the higher concentration gradient at the bottom of the root exclusion layer due to the decreased rate of CO_2 production above this depth. Consequently, F_a, calculated as F_{0c} measured in control (non-disturbed) plots minus F_{0re} measured in root exclusion plots, is underestimated. We describe an analytical model, derived from the soil CO_2 production and diffusion equation, to obtain correct estimates of F_a measured using small-area root exclusion plots. The analytical model requires knowledge of depth distribution of soil CO_2 diffusivity and source strength as inputs.
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1. Introduction

Because soils contain as much as or more carbon than that contained in the atmosphere and live biomass together (Eswaran et al., 1993), soil CO_2 efflux (F_0) has been widely measured under different ecosystems and environmental conditions. Soil CO_2 is the product of decomposition of plant litter and soil organic matter, the heterotrophic respiration (F_h), and from root respiration including respiration of symbiotic microbes and mycorrhizae that feed on root exudates, the autotrophic respiration (F_a). Although F_0 has received considerable attention in recent decades, much less is known about the relative contributions of F_h and F_a to F_0, and our understanding of how they will respond to global warming is poor. The two components of F_0 can have different responses to temperature and soil water content (Boone et al., 1998; Lee et al., 2003; Lavigne et al., 2004), thus the contribution of these components needs to be understood in order that the implications of environmental change for soil carbon cycling and sequestration can be evaluated (Hanson et al., 2000).

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Estimates of F_h are also required for estimating the net primary productivity (NPP) of an ecosystem from eddy covariance measurement of net ecosystem exchange (NEE), i.e. NPP = $-$NEE + F_h.

The contribution of F_a to F_0 has been reported to vary from 10% to as much as 90% for both forest and non-forest ecosystems (Hanson et al., 2000; Xu et al., 2001). Part of this variability may be due to differences in ecosystems, species, or developmental stages (Hanson et al., 2000; Hogberg et al., 2001). However, much of the variation has been attributed to problems associated with measurement techniques (Hanson et al., 2000), each with a unique set of limitations (Rochette et al., 1999). Hanson et al. (2000) reviewed methods and observations for partitioning F_0 into F_h and F_a and concluded that more work is required to refine methods and interpretations.

The trenching method of root exclusion has been widely used for separating F_0 into F_h and F_a, particularly in forest ecosystems (Bowden et al., 1993; Kelting et al., 1998; Epron et al., 1999; Hanson et al., 2000). In this method, roots are severed by digging a trench around the plot and the trench is lined with heavy-duty polyethylene sheet, landscape fabric or tarpaulin to prevent growth of roots into the plot. F_a is estimated from the difference between measured CO_2 effluxes at nearby undisturbed locations and in the trenched plots. There are concerns with this technique that have been identified and investigated, e.g. (a) disturbance effect due to trenching (e.g. Edwards, 1975; Blet-Charaudeau et al., 1990; Ewel et al., 1987; Bowden et al., 1993), (b) influence of residual decomposing roots (e.g. Lavigne et al., 2003) and (c) differences in soil water regime between the trenched and control plots (e.g. Edwards, 1975; Hanson et al., 1993; Thierron and Laudelout, 1996). However, one aspect that seems to have been overlooked in all these studies is the increased contribution of CO_2 to the measured efflux in the root exclusion plot from below the root exclusion depth, as explained below.

A review of the literature indicates that depth of root exclusion with trenching has varied among ecosystems, e.g. 30 cm in Balsam fir (Lavigne et al., 2003, 2004), 40 cm in cool-temperate deciduous forest (Lee et al., 2003), and 100 cm in wet tropical forest (Li et al., 2004) and some other ecosystems (Ewel et al., 1987; Bowden et al., 1993; Epron et al., 1999). Also, in most of these studies, the size of the root exclusion plots is relatively small, e.g., 60 cm × 60 cm in Lee et al. (2003), 1.4 m × 1.4 m in Lavigne et al. (2003, 2004), and 1.5 m × 2 m in Epron et al. (1999). None of these studies report on the depth distribution of soil organic matter or roots. Though both roots and soil organic matter are known to decrease with soil depth either exponentially or with a power law function, small amounts of soil organic matter and even fine roots may be present below the trenching depth (Trumbore et al., 1995; Nepstad et al., 1994). These factors, combined with low diffusivity, may result in high soil CO_2 concentrations at these depths.

Also missing in the above-mentioned root exclusion studies is any information on water table depth and depth of soil or any impermeable layer, all of which affect the CO_2 concentration and concentration gradient at deeper depths. High CO_2 concentrations and significant concentration gradients are generally observed below the 50 cm depth in forest soils, e.g. concentrations of the order of 10,000 ppm at the 50 cm depth (Jassal et al., 2005; Suwa et al., 2004; Takahashi et al., 2004; Trumbore et al., 1995) and significant concentration gradients at the 1 m depth (Drewitt et al., 2005; Jassal et al., 2004; Suwa et al., 2004; Takahashi et al., 2004; Trumbore et al., 1995). Root exclusion, especially in small-area trenched plots is not likely to alter the soil CO_2 concentrations at or below the depth of root exclusion, due to lateral diffusion (Susfalk et al., 2002).

Although CO_2 fluxes in soils below 50 cm depth are generally small compared to CO_2 fluxes in the upper layer (Jassal et al., 2004, 2005; Davidson and Trumbore, 1995; Sombroek et al., 1993), we hypothesize that the upward CO_2 flux from below the root exclusion layer in root exclusion plots will be greater than in control plots due to root exclusion decreasing the source strength (rate of soil CO_2 production), which leads to an increased concentration gradient at the bottom of the root exclusion layer (Fig. 1). This may significantly affect the estimate of autotrophic soil respiration obtained by subtracting measured efflux in root exclusion plots from that in control plots. The objectives of this paper are to: (i) show that soil CO_2 concentrations immediately below the trenching depth are nearly the same as that at the same depth in the control plot, (ii) show that the contribution of the upward flux at the depth of root exclusion in small-area root exclusion plots is increased due to decreased source strength in the absence of roots, and that this results in an underestimation of the autotrophic component of soil respiration and (iii) describe a method for correcting heterotrophic and autotrophic soil respiration measured using the small-area trenched plot technique.

2. Theory

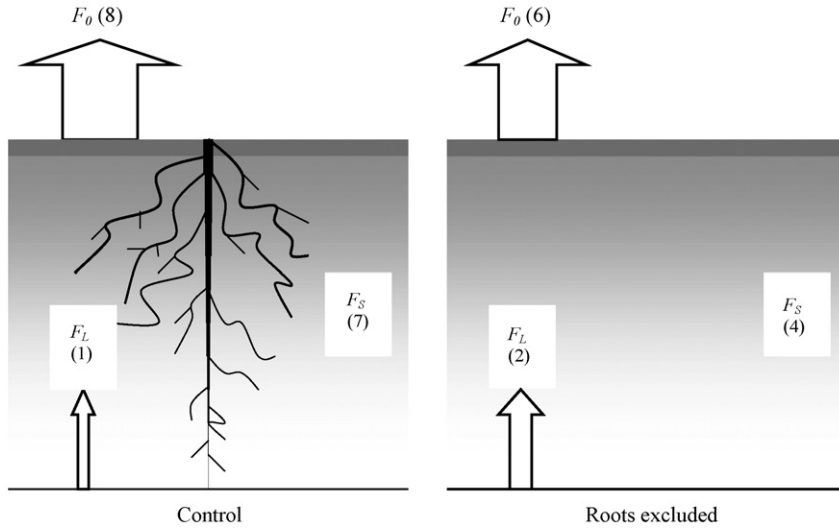Under most field conditions, when changes in barometric pressure are small, transport of CO_2 in soil

Fig. 1. Schematic representation of the control and root exclusion plots illustrating our hypothesis that the difference between the surface efflux (F_0) in the control and root exclusion plots is smaller than the difference in their source strengths (F_S) because of higher flux at the lower boundary (F_L) in the latter owing to an increase in the magnitude of the CO_2 concentration gradient with decrease in source strength. The intensity of the grey color indicates the organic matter content distribution in the soil. The values in parenthesis are relative to 8, which is the CO_2 efflux from a typical forest-floor, and are given for reference only.

is mainly by diffusion in the air-filled pores, and steady state conditions generally exist with respect to CO_2 production and its transport (Jassal et al., 2005, 2004; Amundson et al., 1998). Under steady state conditions, the vertical divergence of the CO_2 flux is equal to the rate of CO_2 production, which can be expressed as $\partial F/\partial z = S$, where $F = -D\,\partial C/\partial z$ is the CO_2 flux (mol m^{-2} s^{-1}), positive upwards, D the effective diffusivity (m^2 s^{-1}), C the CO_2 concentration in the soil air (mol m^{-3}), z the soil depth (negative) (m), and S is the rate of CO_2 production (positive) in the soil (mol m^{-3} s^{-1}) resulting from both root respiration and soil organic matter decomposition. We have observed that both S and D sharply decrease with depth following either an exponential or a power law function of soil depth (Jassal et al., 2005). We consider both D and S to vary with depth as $D = D_0(-z)^m$ and $S = S_0(-z)^n$ (see Fig. 2), respectively, where D_0 and S_0 are the respective values at the soil surface, and m and n lie between -1 and 0. If the depth of root exclusion is L where the CO_2 concentration is C_L and the upward flux of CO_2 from below that depth is F_L, the solution to the diffusion equation: $\partial F/\partial z = S$ can be obtained by integrating it with respect to z twice and imposing the boundary conditions:

$$C = C_L, \qquad z = -L \tag{1}$$

and

$$C = C_0, \qquad z = 0 \tag{2}$$

which, upon substituting $S_0 = (n + 1)(F_0 - F_L)/L^{n+1}$, where F_0 is the surface efflux, gives:

$$F_L = \frac{n + 2 - m}{L^{1-m}} D_0(C_L - C_0) - \frac{n+1}{1-m} F_0 \tag{3}$$

Since by definition $F_L = F_0 - F_S$, where F_S is the source strength, i.e. the total CO_2 flux generated within the soil, in the 0–L layer, Eq. (3) can be written as:

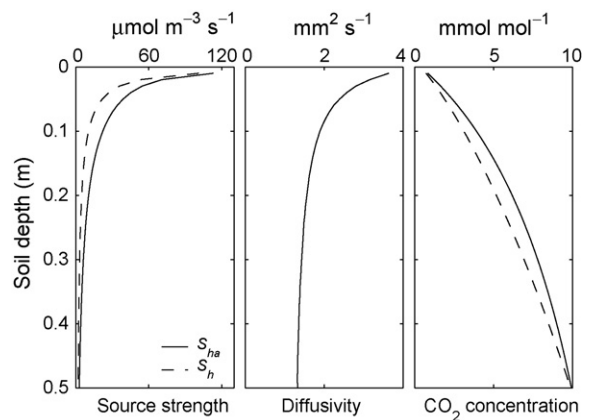$$F_L = -\frac{n+1}{n+2-m} F_S + \frac{1-m}{L^{1-m}} D_0(C_L - C_0) \tag{3a}$$

Fig. 2. Typical depth distributions of source strength (CO_2 production), diffusivity and soil CO_2 concentration, based on model simulations using measured soil organic matter, water content, bulk density, and roots in a 55-year-old Douglas-fir soil. S_{ha} refers to the total source strength from heterotrophic and autotrophic soil respiration, and S_h refers to the source strength following root exclusion.

and F_S, the true soil respiration in the 0–L layer, in terms of F_0 and ($C_L - C_0$) as:

$$F_S = (n + 2 - m)\left(\frac{F_0}{1 - m} - \frac{D_0(C_L - C_0)}{L^{1-m}}\right) \qquad (4)$$

which can also be written as:

$$F_0 = \frac{1 - m}{n + 2 - m}F_S + \frac{1 - m}{L^{1-m}}D_0(C_L - C_0) \qquad (4a)$$

Using Eq. (4), we can estimate true heterotrophic soil respiration and total soil respiration in the 0–L soil layer, hereinafter referred to as F_{Sh} and F_{Sha}, respectively, using measured surface effluxes in the trenched and control plots, i.e. F_{0re} and F_{0c}, respectively. Here C_L is the measured CO_2 concentration at depth L, C_0 is the CO_2 concentration at the soil surface, and D_0 can be estimated from knowledge of air-filled porosity near the soil surface (Jassal et al., 2005). It is assumed that D_0, m and n are not altered by root exclusion, though, however, S_0 in the root exclusion plot will be smaller than in the control plot.

Special cases of D and S distributions can be studied by setting values of the parameters m and n accordingly, e.g. by setting $m = n = -1$ when both D and S decrease linearly with increasing depth so that $D = -D_0/z$ and $S = -S_0/z$, and setting $m = n = 0$ when both D and S are uniformly distributed in the soil profile.

Remember that if the trenching depth extends to a layer such as bedrock or water table that is practically impermeable to gas (CO_2) flow, $F_L = 0$ so that $F_0 = F_S$, i.e. the surface efflux will always be equal to the source strength. In such a case, the above theory is not applicable and true autotrophic respiration can be obtained directly from the difference in measured effluxes from the control and root exclusion plots. Interestingly, in this case Eq. (3) can be used by setting $F_L = 0$ to obtain soil CO_2 concentration (C_L) at the lower impermeable boundary at depth L as $C_0 + (n + 1)L^{1-m}F_0/[(1 - m)(n + 2 - m)D_0]$ or $C_0 + LF_0/(2D_0)$ for conditions of $m = n = 0$.

Eq. (3a) shows that for a given C_L, F_L will be higher when F_S is reduced due to root exclusion. This we validate, along with Eq. (4a), with laboratory measurements and simulations using a multi-layer numerical model of CO_2 production and transport in soil. We then demonstrate the use of Eq. (4) in calculating F_{Sa} and F_{Sh} using measurements from a root exclusion study in a Douglas-fir stand.

3. Methods

3.1. Laboratory column studies

To verify our hypothesis that contribution of F_L to measured CO_2 efflux in root exclusion plot is increased when the source strength is decreased with root exclusion (Fig. 2), we measured soil CO_2 efflux in two identical soil cores differing in source strength. Two stainless steel cylinders, 10 cm long with an internal diameter of 11 cm, were packed with sandy loam soil at a volumetric water content of $0.28\ m^3\ m^{-3}$ to a bulk density of $1.53\ Mg\ m^{-3}$. The two soil cores with same soil, soil water content and bulk density should exhibit identical air-filled porosities and therefore similar diffusivity characteristics. One soil core was allowed to dry under a fan for 24 h and loss of soil water was determined by weighing the core before and after drying. This loss in soil water was recovered by adding an equal amount of 1% glucose + 0.1% NH_4NO_3 solution. This was done to increase soil CO_2 source strength in that core. The two cores, named low source strength and high source strength, respectively, were then wrapped in polythene sheet and stored at room temperature for 4 days so that the water would be uniformly redistributed. The source strength in each core was determined by closing the lower end of the core and measuring the soil CO_2 efflux under steady state conditions, using the experimental set-up described in Jassal et al. (2005). Effluxes from the two cores were also measured with the lower end exposed to different known CO_2 concentrations similar to those encountered in the field. Steady-state conditions were achieved within an hour of exposing the lower end of the soil core to a given CO_2 concentration, and the reported effluxes are mean of four or five measurements after steady-state conditions were achieved. Source strengths measured about 1 h after the exposures of the soil to high CO_2 concentrations were within 5% of those measured before exposure to high CO_2 concentrations. The CO_2 efflux was obtained by measuring the rate of increase of CO_2 concentration during a 2 min interval in a chamber placed over the upper end of the soil column. Air was circulated through the chamber and an infrared gas analyzer (IRGA) (Model LI-820, LI-COR Inc., Lincoln, NE, USA) using a small diaphragm pump (Model TD-4X2N, Brailsford Co., NY, USA). A Vaisala HMP 35-C Humicap humidity sensor (and thermistor) was used to measure water vapour concentration in the sample air to correct the CO_2 efflux for dilution effects. Care was taken while placing the sampling chamber over the soil column to avoid creating static pressure differences across the two ends of the soil column, which could result in

pressure pumping, i.e. losses by mass flow (Jassal et al., 2005).

3.2. Simulation experiments

We also conducted simulation experiments with our multi-layer numerical model (Jassal et al., 2004) using measured soil organic matter content and root density distributions in a 55-year-old Douglas-fir stand (same as used in our field experiment described below). In the model, CO_2 produced from microbial decomposition of soil organic matter and root respiration is allowed to diffuse in the gaseous phase. The production of CO_2 is determined by the amount and type as well as distribution in the soil profile of organic matter and roots, and their respective rate constants, depending on soil water content and temperature. Model runs were made with the CO_2 production and transport module for a 50 cm deep soil profile. The initial conditions were known depth distributions of soil temperature and volumetric water content, and an approximate profile of CO_2 concentration in soil air that depended on the treatment studied. With a distance step of 1 cm (i.e. 50 soil layers) and a time step of 30 min, soil CO_2 production and transport reached steady state after a 24 h simulation run.

In the first simulation experiment, we studied the effect of different soil CO_2 concentrations at the 50 cm depth (C_L) on surface efflux and the component fluxes in the control and root exclusion treatments, assuming that source strength (shown in Fig. 2) does not vary with C_L. In the second simulation experiment, with a

Fig. 3. Time series of measured soil CO_2 concentrations at the 50 cm depth in the root exclusion and control plots along with time series of soil and air temperatures and rainfall in a 55-year-old Douglas-fir forest. The root exclusion plot measuring 50 cm × 50 cm × 50 cm deep was established on DOY 173 (June 22).

constant soil CO_2 concentration of 10 mmol mol^{-1} at the 50 cm depth, we studied the effects on different components of soil CO_2 efflux of the following treatments: (1) control, (2) no roots (root exclusion in the top 50 cm soil) and (3) no roots and no soil organic matter in the top 50 cm soil, i.e. zero source strength.

3.3. Field measurements of soil CO_2 concentrations and effluxes

A 50 cm × 50 cm trenched plot was established in the 55-year-old Douglas-fir stand by digging a trench around the boundary to 50 cm depth (approximately the bottom of the root zone). The inside wall of the trench was lined with a 100 μm thick polyethylene film and the trench was backfilled layer wise to avoid disturbance to nearby control plots. Also, before backfilling, three Vaisala infrared CO_2 sensors (model GMM-221, Vaisala Oyj., Helsinki, Finland), covered with Teflon socks (see Jassal et al., 2005), were inserted into horizontal holes made by augering into one wall of the trench. One sensor was positioned in the middle of the root exclusion plot just below the trenching depth (50 cm) and the other two were placed at the same depth but about 50 cm away in the adjacent control plots on opposite sides of the trenched plot. The sensors were connected to a CR-21X data logger (Campbell Scientific Inc., Logan, UT, USA), which was programmed to excite the sensors for the last 5 min of each hour (to avoid localized heating, Jassal et al., 2004), and soil CO_2 concentrations were continuously measured over the next five months. Six PVC collars 5 cm long and 10 cm internal diameter were inserted 2 cm into the ground – two at each of the three locations immediately above the locations of CO_2 sensors. Soil CO_2 efflux was measured every 2–4 weeks by placing a 1.5 dm^3 chamber on the collars and measuring the rate of increase of CO_2 concentration over 2 min periods with a portable infrared gas analyzer. Any plants growing in the root exclusion plot and inside the collars were occasionally clipped at the ground surface to prevent any new root growth and influence on soil CO_2 effluxes.

4. Results and discussion

Field measurements in a 55-year-old Douglas-fir stand showed that soil CO_2 concentrations at immediately below the root exclusion depth (50 cm) in a 50 cm × 50 cm root exclusion plot were generally within 5% of that at the same depth in the control plot (Fig. 3). Absence of roots reduces the source strength and hence the soil CO_2 concentrations in the root
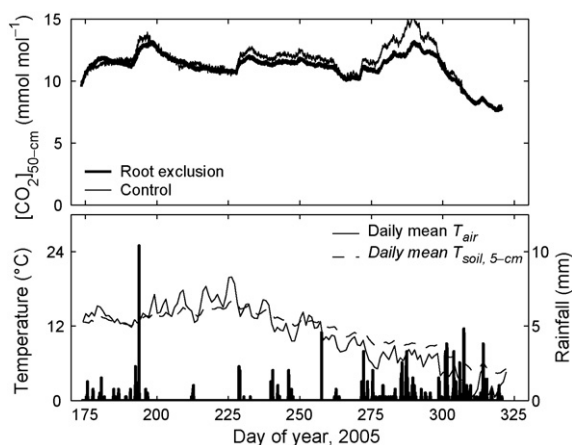
Table 1
Effect of CO_2 concentration at the lower end of a 10 cm long soil column on measured surface CO_2 efflux (F_0) and inferred flux at the lower boundary (F_L) in two soil cores of different source strengths

CO_2 concentration at the lower boundary (mmol mol^{-1})	High source strength[a]			Low source strength[b]		
	F_0 (µmol m^{-2} s^{-1})	F_L (µmol m^{-2} s^{-1})	F_L/F_0	F_0 (µmol m^{-2} s^{-1})	F_L (µmol m^{-2} s^{-1})	F_L/F_0
8.1 ± 0.1	4.6	2.0	0.43	4.0	2.8	0.70
9.9 ± 0.1	5.4	2.8	0.52	4.8	3.6	0.75
12.4 ± 0.2	6.6	4.0	0.61	6.1	4.9	0.80
16.4 ± 0.3	7.9	5.3	0.67	7.5	6.3	0.84
19.2 ± 0.3	9.1	6.5	0.71	8.9	7.7	0.86

[a] 2.6 µmol m^{-2} s^{-1}.
[b] 1.2 µmol m^{-2} s^{-1}.

exclusion plot. This results into a concentration gradient between the bottom of the root exclusion plot and rest of the undisturbed soil. As a consequence, lateral diffusion follows and masks any difference in the soil CO_2 concentrations at the bottom of the root exclusion plot and the adjoining undisturbed soil.

The laboratory column study (Table 1) showed that the surface soil CO_2 efflux in both the low and high source strength soil cores increased with increasing CO_2 concentration at the lower boundary with corresponding increases in the upward flux (F_L) at the lower boundary. Also, for the same C_L, F_L was consistently higher in the low source strength core than in the high source strength core, both in terms of magnitude and as a fraction of F_0 (Table 1). These results are consistent with Eq. (3a), which shows that for a given C_L, F_L will be higher when F_S is smaller, and that F_L will increase with increasing C_L.

Results in Fig. 4 confirm Eq. (4a), which shows that for a given F_S, the efflux (F_0) is linearly related to ($C_L - C_0$). It is clear from Eq. (4a) that in the case of repacked soil cores, for which $m = n = 0$, $F_0 = F_S/2 = -F_L$ when ($C_L - C_0$) = 0, i.e. when both ends of a soil column, with uniform distribution of D and S, are exposed to ambient air CO_2, one half of the total CO_2 produced (F_S) will be emitted at $z = 0$ and the other half at $z = L$. Accordingly, values of intercepts of the regression lines (Fig. 4) show $F_S/2$ for the high and low source strength soil columns to be 1.63 and 0.71 µmol m^{-2} s^{-1}, respectively. The values of $F_S/2$, obtained by measuring F_S with one end of the soil columns closed, of 1.30 and 0.60 µmol m^{-2} s^{-1}, respectively, were within the 95% confidence bounds (Wald test, $p = 0.21$ and 0.11, respectively) of the intercept values. These results validated the theory and proved the hypothesis that, for a given C_L, the contribution of the upward CO_2 flux at the lower boundary is greater when the source strength is lower as would be the case with root exclusion. This we further show below by simulating root exclusion using the multi-layer numerical model.

Results of the simulation experiment (Fig. 5) show that both F_0 and F_L in the control as well as in the root exclusion plots linearly increased with increasing ($C_L - C_0$). With F_S constant and the slopes of the F_0 and F_L lines the same, any increase in the surface efflux is due to an equal increase in F_L, which is due to an increase in the magnitude of the concentration gradient at the 50 cm depth. The intercepts of 6.14 and 3.24 for the F_0 versus ($C_L - C_0$) lines in the control and root exclusion treatments, respectively, and a common slope of 0.38 were very similar to 6.12, 3.18 and slope of 0.40, respectively, obtained from the analytical model, Eq. (4a). The latter were calculated using estimated values of m and n of -0.24 and -0.55, respectively (Jassal et al., 2005) and D_0 calculated using the 0–1 cm soil water content and bulk density. Also, F_L, at a given
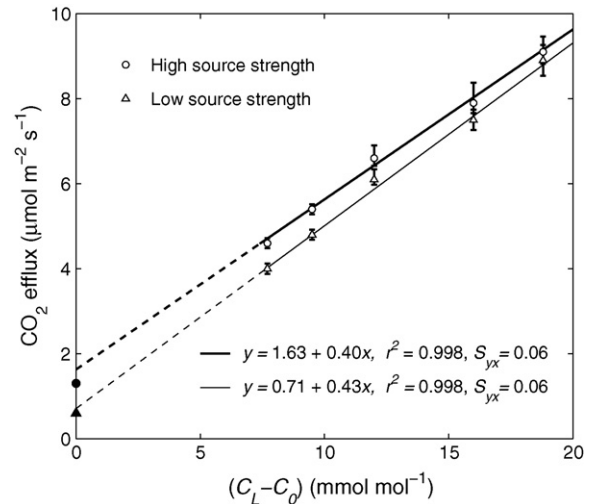

Fig. 4. Relationship between soil CO_2 efflux and difference in CO_2 concentration at the lower boundary (C_L) and the soil surface (C_0) in two 10 cm long soil columns of high and low source strength. The solid points are one-half of the respective source strengths measured by closing one end of the soil columns, not included in the regression analysis and are shown only for comparison. Error bars indicate variation around the mean.
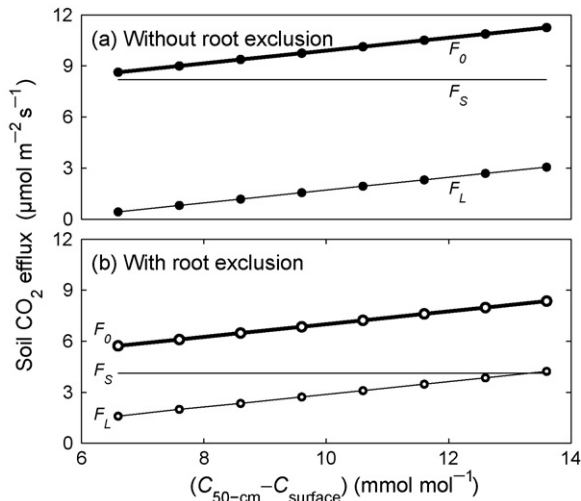
Fig. 5. Effect of soil CO_2 concentration at the 50 cm depth on the surface CO_2 efflux (F_0) and the contribution to it by the flux at the 50 cm depth (F_L) in control and root exclusion plots. F_S is the source strength due to the production of CO_2 in the soil between 0 and 50 cm depths. The results were obtained from a simulation experiment using the process-based multi-layer numerical model of CO_2 production and transport in soil (Jassal et al., 2004).

C_L, was always higher in the root exclusion treatment than in the control and still higher in the zero source treatment (see Table 2). At $(C_L - C_0) = 0$, F_L for the control and root exclusion treatments is -2.05 and -0.86 μmol m^{-2} s^{-1}, respectively, i.e. in the downward direction, which when subtracted from the respective intercepts of F_0 versus $(C_L - C_0)$ lines give 8.17 and 4.04 μmol m^{-2} s^{-1}, which agree very well with the independently determined source strengths of 8.19 and 4.13 μmol m^{-2} s^{-1}, respectively (see Table 2). Further simulations (Table 2) show that at a given CO_2 concentration of 10 mmol mol^{-1} at the 50 cm depth, F_0 decreased from 9.75 μmol m^{-2} s^{-1} in the control to 6.85 and 3.61 μmol m^{-2} s^{-1} in the root exclusion and

zero source strength treatments, respectively, while F_L increased from 1.56 μmol m^{-2} s^{-1} to 2.73 and 3.61 μmol m^{-2} s^{-1} in the same order. Thus the contribution of the upward flux at the 50 cm depth to the surface efflux increased with decreasing source strength in the 0–50 cm soil. Ignoring the contribution of this increase in flux and interpreting the root exclusion experiment in the usual way, the estimate of the ratio of heterotrophic to total soil respiration would be 6.85/9.75, i.e. 70%. This is nearly 1.5 times higher than the actual ratio for the 0–50 cm soil layer ($F_{Sh}/F_{Sha} = 4.13/8.19$), which is 50%. We obtained very good estimates of the true fluxes (F_S) originating in the 0–50 cm soil layer in all the treatments (Table 2) when using Eq. (4), and this resulted in a correct estimate of the relative contribution of heterotrophic soil respiration. Regarding the ratio of autotrophic to total soil respiration, its estimate from measurements of F_0 and F_h will be $(9.75 - 6.85)/9.75$, i.e. 29%. However, using Eq. (4), the true F_{Sa} in the 0–50 cm soil layer is 4.05 μmol m^{-2} s^{-1}, and assuming it is negligible below the 50 cm depth, which is reasonable, the true root contribution will be 4.05/9.75, i.e. 42%.

Our field measurements confirmed the above results. Mean F_a obtained from differences in the measured CO_2 effluxes in the control and root exclusion plots, was only 24% of the total efflux (Table 3). Calculations using Eq. (4) showed that this estimate of autotrophic soil respiration for the 0–50 cm soil layer increased to 39%. The latter compares very well with 40% reported for temperate forests globally (Bond-Lamberty et al., 2004). Thus the traditional way of obtaining autotrophic soil respiration by subtracting measured efflux in root exclusion plots from the efflux in undisturbed plots results in an overestimation of heterotrophic and underestimation of autotrophic contributions. This occurs because of increased contribution of flux from below the root exclusion layer as a result of the decrease

Table 2

Simulated[a] contribution of different components of soil respiration to surface soil CO_2 efflux (μmol m^{-2} s^{-1}) at a constant concentration of 10 mmol mol^{-1} CO_2 at the 50 cm depth

Parameter	Control	No roots (root exclusion)	No roots, no soil organic matter
F_{Sh} (heterotrophic)	4.13	4.13	0
F_{Sa} (autotrophic)	4.06	0	0
F_{Sha} ($F_{Sh} + F_{Sa}$)	8.19	4.13	0
F_0 (surface efflux)	9.75	6.85	3.61
F_L (flux from below 50 cm depth)	1.56	2.73	3.61
F_L/F_0 (%)	16	40	100
F_S calculated with Eq. (4)[b]	8.13	4.05	0

[a] Using the multi-layer numerical model (Jassal et al., 2004).

[b] Using m and n values of -0.24 and -0.55, respectively, obtained from the depth distributions of source strength and diffusivity shown in Fig. 2. Diffusivities are calculated from air-filled porosity (ε) using $D = 1.2\varepsilon^{2.3}$ (Jassal et al., 2005).

Table 3
Mean soil CO_2 effluxes (μmol m^{-2} s^{-1}) in control (F_0) and root exclusion (F_h) plots, and uncorrected (F_a/F_0) and corrected (F_{Sa}/F_{Sha}) (calculated using Eq. (4)) fraction of autotrophic soil respiration in a 55-year-old Douglas-fir forest

Measurements					Calculations[a]			
Date[b]	F_0	F_h	$F_a = F_0 - F_h$	F_a/F_0	F_{Sha}	F_{Sh}	$F_{Sa} = F_{Sha} - F_{Sh}$	F_{Sa}/F_{Sha}
July 8	4.24	3.26	0.98	0.22	3.63	2.27	1.36	0.37
July 21	4.88	3.49	1.39	0.26	4.45	2.60	1.85	0.41
August 17	5.03	3.95	1.08	0.21	4.54	3.07	1.47	0.33
August 30	5.94	4.04	1.90	0.31	5.93	3.46	2.47	0.42
September 21	3.71	2.88	0.83	0.22	2.99	1.86	1.13	0.38
November 17	1.62	1.25	0.34	0.23	1.20	0.70	0.50	0.42
Mean	4.24	3.14	1.09	0.24	3.79	2.33	1.46	0.39

[a] Using Eq. (4) with m and n values of -0.24 and -0.55, respectively, obtained from the depth distributions of source strength and diffusivity shown in Fig. 2. Diffusivities are calculated from air-filled porosity (ε) using $D = 1.2\varepsilon^{2.3}$ as explained in Jassal et al. (2005).

[b] Root exclusion plot was established on June 22, 2005.

in source strength in this layer, and holds irrespective of whether some roots exist below the root exclusion depth. Assuming no roots existed below the 50 cm depth, data in Table 3 suggest that net F_a (mean for the growing season) obtained using Eq. (4) is $(3.79 - 2.33)/4.24$, i.e. 34% of the total soil respiration.

Using Eq. (4), it can be further shown that if no roots exist below the root exclusion depth, i.e. $F_{Sa} = F_a$, the true autotrophic soil respiration, can be directly obtained from $F_{Sa} = F_{Sha} - F_{Sh}$ (i.e. subtracting Eq. (4) written for F_{Sh} from that written for F_{Sha}), which gives:

$$F_a = F_{Sa} = \frac{n+2-m}{1-m}(F_{0c} - F_{0re}) \quad (5)$$

where F_{0c} and F_{0re} are the measured effluxes in the control and the root exclusion plots, respectively. Eq. (5), which does not require as input any information on measured soil CO_2 concentration, can be directly used as a means of correcting autotrophic soil respiration for the increased flux from below the root exclusion layer when no roots exist below the trenching depth. It requires knowledge of m and n that describe the depth distribution of soil CO_2 diffusivity and CO_2 source strength, respectively, in a given ecosystem. Because both root density and soil organic matter content decrease exponentially with depth, Eq. (5) should still work satisfactorily when some roots are present below the depth of root exclusion. This method has the advantage as the small-area root exclusion plots can be conveniently obtained by pushing metallic cylinders (having the same diameter as the PVC collars) into soil (Kelting et al., 1998) to the depth of rooting, and, therefore, makes it possible to cover large areas with a view to study and account for spatial variability in heterotrophic and autotrophic soil respiration. Using

Eq. (5), our measurements (Table 3) provided an estimate of F_a as 35% of total soil respiration, compared to uncorrected 24% obtained by the usual subtraction method. However, this estimate of 35% is somewhat higher than that obtained using Eq. (4) (34%) under the same assumptions, i.e. no roots existed below the trenching depth. This discrepancy is likely due to the uncertainty in the computation of D_0 in Eq. (4) from the measured soil water contents in the 0–2 cm layer, and in the measurement of C_L.

Regarding sensitivity to the values of m and n, calculations using Eq. (5) show that for an uncertainty of $\pm 10\%$ in m and n, individually or both together, autotrophic soil respiration is affected by $\pm 4\%$. It is interesting to note that when both D and S are uniformly distributed in the soil profile, i.e. $m = n = 0$, the correct F_a will be twice that obtained from direct subtraction of F_{0re} from F_{0c}, while no correction will be required if both D and S vary inversely with depth, i.e. when $m = n = -1$. Values of the parameters m and n can be estimated from the depth distributions of air-filled soil porosity, which determines D, and soil organic matter content, respectively, shown in Fig. 2.

5. Conclusions

Field measurements showed that soil CO_2 concentrations just below the root exclusion layer in a small-area root exclusion plot (50 cm $\times$ 50 cm) were nearly the same as those at the same depth in nearby undisturbed soil. A laboratory column study and simulations using a multi-layer numerical model showed that for the same CO_2 concentration at the bottom of a soil column, the magnitude of the upward CO_2 flux at the lower boundary increased with decrease in the CO_2 source strength in the soil column. These

results confirmed the hypothesis that the contribution of the upward flux at the base of the root exclusion layer (i.e. the trenching depth) in small-area root exclusion plots is higher as a result of the reduction in source strength due to the absence of root respiration. As a consequence, the relative contribution of the auto-trophic component of soil respiration, calculated as the efflux measured in control plots minus the efflux measured in root exclusion plots, is underestimated. Based on the soil CO_2 production and the diffusion equation, we derive an analytical solution, Eq. (5), which can be used to calculate true autotrophic and heterotrophic soil respiration using measured CO_2 effluxes from small-area root exclusion and control plots. This requires knowledge of D and S distributions, which can be estimated from the measured vertical distributions of volumetric water content and organic matter content in the soil.

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References

Amundson, R., Stern, L., Baisden, T., Wang, Y., 1998. The isotopic composition of soil and soil-respired CO_2. Geoderma 82, 83–114.

Blet-Charaudeau, C., Muller, J., Laudelout, H., 1990. Kinetics of carbon dioxide evolution in relation to microbial biomass and temperature. Soil Sci. Soc. Am. J. 9, 1324–1328.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration. Global Change Biol. 10, 1756–1766.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Mellilo, J.M., Garrison, J.B., 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res. 23, 1402–1407.

Davidson, E.A., Trumbore, S.E., 1995. Gas diffusivity and production of CO_2 in deep soils of the eastern Amazon. Tellus B 47, 550–565.

Drewitt, G.B., Black, T.A., Jassal, R.S., 2005. Using measurements of soil CO_2 efflux and concentrations to infer the depth distribution of CO_2 production in a forest soil. Can. J. Soil Sci. 85, 213–221.

Edwards, N.T., 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Sci. Soc. Am. J. 39, 361–365.

Epron, D., Farque, L., Lucot, E., Badot, P.-M., 1999. Soil CO_2 efflux in a beech forest: the contribution of root respiration. Ann. For. Sci. 56, 289–295.

Eswaran, H., van den Berg, E., Reich, P., 1993. Organic carbon in soils of the world. Soil Sci. Soc. Am. J. 57, 192–194.

Ewel, K.C., Cropper, W.P., Gholz, H.L., 1987. Soil CO_2 evolution in Florida slash pine plantations II. Importance of root respiration. Can. J. For. Res. 17, 330–333.

Hanson, P.J., Wullschleger, S.D., Bohlman, S.A., Todd, D.E., 1993. Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest. Tree Physiol. 13, 1–15.

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.

Hogberg, P., Nordgren, A., Buchmann, N., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792.

Jassal, R.S., Black, T.A., Drewitt, G.B., Novak, M.D., Gaumont-Guay, D., Nesic, Z., 2004. A model of the production and transport of CO_2 in soil: predicting soil CO_2 concentrations and CO_2 efflux from a forest floor. Agr. For. Meteorol. 124, 219–236.

Jassal, R.S., Black, T.A., Novak, M.D., Morgenstern, K., Nesic, Z., Gauymont-Guay, D., 2005. Relationship between soil CO2 concentrations and forest-floor CO2 effluxes. Agr. For. Meteorol. 130, 176–192.

Kelting, D.L., Burger, J.A., Edwards, G.S., 1998. Estimating root respiration, microbial respiration in the rhizosphere, and root-free soil respiration in forest soils. Soil Biol. Biochem. 30, 961–968.

Lavigne, M.B., Foster, R.J., Goodine, G., 2004. Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. Tree Physiol. 24, 415–424.

Lavigne, M.B., Boutin, R., Foster, R.J., Goodine, G., Bernier, P.V., Robitaille, G., 2003. Soil respiration responses to temperature are controlled more by roots than by decomposition in Balsam fir ecosystems. Can. J. For. Res. 33, 1744–1753.

Lee, M., Nakane, K., Nakatsubo, T., Koizumi, H., 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. Plant Soil 255, 311–318.

Li, Y., Xu, M., Sun, O.J., Cui, W., 2004. Effects of root and litter exclusion on soil CO_2 efflux and microbial biomass in wet tropical forests. Soil Biol. Biochem. 36, 2111–2114.

Nepstad, D.C., Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., daSilva, E.D., Stone, T., Trumbore, S.E., Viera, S., 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372, 666–669.

Rochette, P., Flanagan, L.B., Gregorich, E.G., 1999. Separating soil respiration into plant and soil components using analysis of natural abundance of Carbon-13. Soil Sci. Soc. Am. J. 63, 1207–1213.

Sombroek, W.G., Nachtergaele, F.O., Hebel, A., 1993. Amounts, dynamics and sequestering of carbon in tropical and subtropical soils. Ambio 22, 417–426.

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.

Suwa, M., Katul, G.G., Oren, R., Andrews, J., Pippen, J., 2004. Impact of elevated atmospheric CO_2 on forest floor respiration in a temperate pine forest. Global Change Biol. 18, GB2013 doi:10.1029/2003GB002182.

Takahashi, A., Hiyama, T., Takahashi, H.A., Fukushima, Y., 2004. Analytical estimation of the vertical distribution of CO_2 production within soil: application to a Japanese temperate forest. Agr. For. Meteorol. 126, 223–235.

Thierron, V., Laudelout, H., 1996. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. Can. J. For. Res. 26, 1142–1148.

Trumbore, S.E., Davidson, E.A., de Camargo, P.B., Nepstad, D.C., Martinelli, L.A., 1995. Belowground cycling of carbon in forests and pastures of eastern Amazonia. Global Biogeochem. Cycle 9, 515–528.

Xu, M., DeBaise, T., Qi, Y., Goldstein, A., Liu, Z., 2001. Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains. California Tree Physiol. 21, 309–318.