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Separating root and soil microbial contributions to soil respiration: A review of methods and observations

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Abstract. Forest soil respiration is the sum of heterotrophic (microbes, soil fauna) and autotrophic (root) respiration. The contribution of each group needs to be understood to evaluate implications of environmental change on soil carbon cycling and sequestration. Three primary methods have been used to distinguish hetero- versus autotrophic soil respiration including: integration of components contributing to *in situ* forest soil CO_2 efflux (i.e., litter, roots, soil), comparison of soils with and without root exclusion, and application of stable or radioactive isotope methods. Each approach has advantages and disadvantages, but isotope based methods provide quantitative answers with the least amount of disturbance to the soil and roots. Published data from all methods indicate that root/rhizosphere respiration can account for as little as 10 percent to greater than 90 percent of total *in situ* soil respiration depending on vegetation type and season of the year. Studies which have integrated percent root contribution to total soil respiration throughout an entire year or growing season show mean values of 45.8 and 60.4 percent for forest and nonforest vegetation, respectively. Such average annual values must be extrapolated with caution, however, because the root contribution to total soil respiration is commonly higher during the growing season and lower during the dormant periods of the year.

Abbreviations: TS_{cer} – total soil CO_2 efflux rate; f – fractional root contribution to TS_{cer}; RC – root contribution to TS_{cer}

Introduction

Manipulation of soils to increase their carbon (C) storage capacity has been proposed as a method for slowing the rate of atmospheric CO_2 increase which is suggested to be primarily responsible for current atmospheric warming (IPCC 1996). Much discussion centers on the feasibility of this approach (Anderson 1991; Dixon & Turner 1991; Jenkinson et al. 1991; Johnson & Kern 1991; Raich & Nadelhoffer 1989; Schlesinger 1990; Smith et al. 1997; Winjum et al. 1992). Recognition that elevated atmospheric CO_2 can lead to

greater below ground C allocation in vegetation (Norby et al. 1995; Thomas et al. 1996) has also lead to the suggestion that forest ecosystems may sequester more soil C as atmospheric levels of CO_2 continue to rise. Other studies suggest that an increase in below-ground C allocation resulting from plant responses to increasing atmospheric CO_2, might may be accompanied by increased CO_2 loss from the soil proportionate to increases in root density (Edwards and Norby 1999; Hungate et al. 1997; Luo et al. 1996).

Experimental verification of changes in soil C resulting from either direct anthropogenic manipulations (i.e., soil C amendments) or atmospheric CO_2 fertilization may require long-term experiments (e.g., Billet et al. 1990; Jenkinson 1991). Alternatively, measurements of total soil CO_2 efflux rates (TS_{cer}) together with data on litter inputs (i.e., leaves, wood, coarse and fine roots) over one or more growing seasons can be used to evaluate soils as sources or sinks of C over shorter periods according to the following equation:

$$\text{Net soil C increment} = \text{Litter inputs} - (TS_{cer} - \text{root respiration}), \quad (1)$$

where the difference between TS_{cer} and root/rhizosphere respiration is the C evolved from heterotrophic consumption of soil C. The loss of soil C as dissolved organic carbon compounds leaching from the soil profile might require modification of equation 1 for application to some ecosystems.

Efflux of CO_2 from the forest soil 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 activity (Edwards et al. 1970). Whereas the activity of soil heterotrophic organisms is proportionate to the decomposition of soil C, CO_2 lost from root and rhizosphere activity is tied to the consumption of organic compounds supplied by above ground organs of plants (Horwath et al. 1994). The fraction of TS_{cer} derived from live roots is independent of soil C pools, and live root contributions to TS_{cer} must be understood before measurements of TS_{cer} can be used to infer rates of long term soil C storage (i.e., solving equation 1). A diagram of the various C fluxes involved in the soil C cycle is shown in Figure 1.

Although, root respiration is clearly a combination of root activity and the activity of microorganisms in the rhizosphere, we don't emphasize this distinction in the current paper. Instead, root respiration is defined to include all processes occurring in the rhizosphere following the definition of Wiant (1967a) who stated that "root respiration includes all respiration derived from organic compounds originating in plants including the respiration of living root tissue, 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." This broad definition lumps

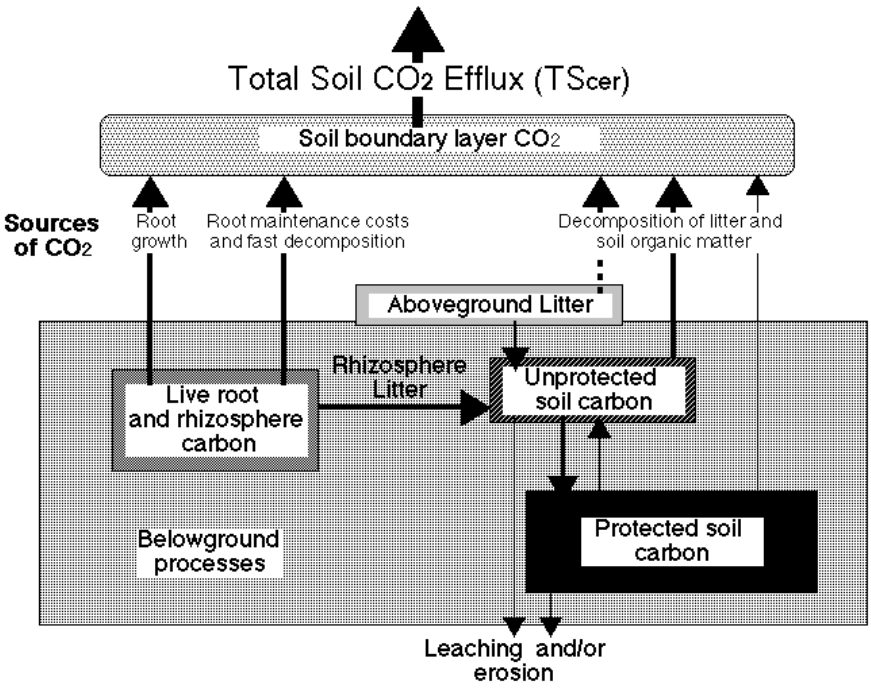

Figure 1. Components of CO_2 efflux from forest soils (TS_{cer}). TS_{cer} from the soil boundary layer to the atmosphere equals CO_2 production from roots, rhizosphere heterotrophs, litter, and soil heterotrophs when steady state conditions are approached. Abnormal turbulence at the soil surface can produce TS_{cer} which exceeds the rate of CO_2 production by the component processes. The dashed line from the surface litter layer indicates a dynamic process highly dependent on litter water content.

many processes that would be interesting to quantify separately, however, current methods limit our ability to do so. The reader is referred to Smart et al. (1995), Swinnen (1994), Cheng et al. (1993, 1994) and Rouhier et al. (1996) for information on root versus microbe contributions to rhizosphere respiration, and to Paterson et al. (1997) for a discussion of methods for quantification of C flow from plants to the rhizosphere.

Although an early review of soil respiration (Turpin 1920) concluded that the primary source of CO_2 efflux from soils was attributable to decomposition by bacteria, later data and analyses suggested that root respiration in soils of forests may commonly exceed the value for decomposition (Wiant 1967a). Anderson (1973) stated that "the principal source of error in soil respirometry *per se* is the CO_2 output of living roots" and Reiners (1963) concluded that root respiration was the likely explanation for CO_2 losses from soils in excess of annual litter inputs. Garrett and Cox (1973) did not quantify the

contribution of roots to TS_{cer} of an oak-hickory forest, but concluded that "most of the CO_2 released from the soil of (their) oak-hickory forest (was) contributed by root respiration and associated microorganisms and not by the decomposition of litter." Toland and Zak (1994) also concluded that the likely reason for no differences in TS_{cer} among intact and clear-cut northern hardwood forests were compensating impacts of reduced root respiration and increased microbial activity in the clear cut plots. The conclusions of the previous authors demonstrates the importance of root and rhizosphere organisms as large contributors to TS_{cer}. A number of studies continue to be published which interpret TS_{cer} as a direct measure of soil heterotrophic processes (Dulohery et al. 1996; Fernandez et al. 1993), or try to develop simple relationships between TS_{cer} and environmental variables (Froment 1972; Jensen et al. 1996) without adequate consideration of the confounding influence of roots/rhizosphere activity.

The primary objective of this paper is to critique methods for quantifying root contributions to total soil CO_2 efflux (RC) and provide recommendations for field application. Secondarily, this paper provides a summary of published estimates of RC from forest and cropland studies. The reader is referred to reviews by Anderson (1973), Singh and Gupta (1977) and Behera et al. (1990) for additional discussion of the components of forest soil respiration.

Methods for quantification of root contribution to TS_{cer} (RC)

The quantification of RC has been addressed using a variety of approaches that can be subdivided into three broad categories: component integration, root exclusion, and isotopic approaches. Each approach is discussed below and estimates of percent RC measured using each of these methods are presented in Table 1. Before each of the methods is discussed, it is important to recognize that estimates of RC will not be useful unless they are based on good measurements of TS_{cer}.

Under constant environmental and boundary conditions, TS_{cer} is equal to CO_2 production in the soil if one can justify minimal losses to deep soil through percolation or inorganic chemical oxidation (Bunt & Rovira 1954; Edwards & Harris 1977). However, many measurement approaches disturb surface equilibrium conditions leading to transient rates of TS_{cer} that can be higher or lower than rates of CO_2 production within the soil. Estimating the contribution of root respiration to total TS_{cer} requires that the initial measurement of total TS_{cer} be as close to the true rate of production within soils as possible. Environmental conditions that limit or accelerate the diffusion of CO_2 from soils or the surface boundary layer (Figure 1) can create nonequilibrium TS_{cer} that differs from soil CO_2 production rates.

Table 1. Published estimates of the percent root/rhizosphere contributions to total soil respiration (RC) by vegetation type and experimental approach. The experimental setting (e.g., field versus laboratory) and the time step for which the data are applicaable (d = 1 day or less, w = week or weeks, m = monthly or seasonal, and a = annual) are also provided.

Vegetation type/ Species	Experimental setting	Approach[1]	RC	Time step	Reference
Forest					
Abies	—	—[2]	30 (citing others)	a	Lieth & Ovellette 1962
Betula	container	Rexcl.	69 summer	m	Minderman & Vulto 1973
"	container	Rexcl.	33–50 winter	m	"
Castenea/Fagus	field	Cint.	20	a	Andersen 1973
Fagus	field	Cint.	5	a	Phillipson 1975
Fagus	field	Rexcl. (gap)	40	d	Brumme 1995
Fagus/Abies	field	—	42 old growth	a	Nakane 1980
Fagus/Picea	field	Iso-^{14}C	40	m	Dörr & Münnich 1987
Fagus/Picea	field	Iso-^{14}C	75 summer	m	Dörr & Münnich 1986
"	field	Iso-^{14}C	25 winter	m	"
Liriodendron	field	Cint.	22–36	a	Edwards & Sollins 1973
Liriodendron	field	Cint.	77	a	Edwards & Harris 1977
Nothofagus	field	Cint.	23	d	Tate et al. 1993
Quercus/Acer	field	Rexcl.	33	a	Bowden et al. 1993
Quercus	field	Rexcl.	84	d	Edwards & Ross-Todd 1983

Table 1. Continued.

Vegetation type/ Species	Experimental setting	Approach[1]	RC	Time step	Reference
Quercus	lab	Cint.	40 Oa horizon	d	De Boois 1974
Quercus	field	—	48	a	Kira 1978
Quercus	field	—	50	a	Nakane & Kira 1978
Quercus	field	Cint.	6–11 (5 cm cores)	d	Coleman 1973
Quercus	field	Rexcl.	90	a	Thierron & Laudelout 1996
Quercus	field	—	48–52 old growth	a	Nakane 1980
Quercus	field	Rexcl.	52 late summer	d	Kelting et al. 1998
Picea mariana	field	Cint.	54 August	d	Uchida et al. 1998
"			6 L horizon	d	"
"			80 FH horizont	d	"
"			43 A horizon	d	"
"			0 E horizon	d	"
Picea mariana	field	Cint.	82	a	Flanagan & Van Cleve 1977
"			80 L horizon	a	"
"			90 H horizon	a	"
Pinus	field	Rexcl.	45–66	w	Wiant 1967b
Pinus elliottii	field	Rexcl.	51 9-y plantation	a	Ewel et al. 1987
Pinus elliottii	field	Rexcl.	62 29-y plantation	a	Ewel et al. 1987

Table 1. Continued.

Vegetation type/ Species	Experimental setting	Approach[1]	RC	Time step	Reference
Pinus taeda	field	Rexcl.	67 in December	d	Edwards 1991
"	field	Rexcl.	78 in March	d	"
"	field	Rexcl.	54 in May	d	"
"	field	Rexcl.	67 in August	d	"
Pinus taeda	field	Iso-^{13}C	49	d	Andrews et al. 1997
Pinus resinosa	field	Rexcl.	40–65	a	Haynes & Gower 1995
Pinus densiflora	field	Rexcl.	47–51 80 year stand	a	Nakane et al. 1983
Pinus ponderosa	field	Cint.	~90	d	Johnson et al. 1994
Populus euramerican	field	I-^{14}C	20	d	Horwath et al. 1994
Populus tremuloides	field	Cint.	60	a	Russel & Voroney 1998
Pseudotsuga (1–y)	chamber	I-^{13}C/^{18}O	28 April	d	Lin et al. 1998
"			12 June	d	"
"			25 August	d	"
"			30 October	d	"
Quercus/Carya	field	Cint.	>50	d	Garret & Cox 1973
Tsuga	field	Rexcl.	37–52	a	Wiant 1967b
Broad-leaved	field	Rexcl.	51	a	Nakane et al. 1996
Hardwood	field	Rexcl.	13–17	a	Catricala et al. 1997

Table 1. Continued.

Vegetation type/ Species	Experimental setting	Approach[1]	RC	Time step	Reference
N. hardwoods	lab	Cint.	~20 litter layer Oe/Oa	d	Hendrickson & Robinson 1984
N. hardwoods	lab	Cint.	43–58 mineral soil	d	Hendrickson & Robinson 1984
Tropical deciduous	field	Cint.	50.5	d	Behera et al. 1990
Tropical forest	field	Cint.	55 litter to 1 m	a	Trumbore et al. 1995
"	field	Cint.	43 1 to 5 m	a	"
Tropical forest	field	—	49 old growth	a	Nakane 1980
Nonforest observations					
Arctic tundra	field	Cint.	50–90	a	Billings et al. 1977
Old field	field/lab	Cint.	13–17 May	d	Coleman 1973 (5 cm cores)
Old field	field/lab	Cint.	8–15 Dec	d	Coleman 1973 (5 cm cores)
Oil palm planting	field	Rexcl.	30–80	a	Lamade et al. 1996
Peat lands	field/lab	Rexcl.	35–45	m	Silvola et al. 1996
Tall Grass prairie	field	Cint.	40	a	Kucera & Kirkham 1971
Pasture grass	field	Rexcl.	53	a	Robertson et al. 1995
Bermuda grass	lab	I-C4/C3	40–100	a	Robinson & Scrimgeour 1995
Grass	field	I-^{14}C	10	m	Dörr & Münnich 1987
Grass	field	I-^{14}C	98 summer	m	Dörr & Münnich 1986

Table 1. Continued.

Vegetation type/ Species	Experimental setting	Approach[1]	RC	Time step	Reference
Grass	field	I-^{14}C	80 winter	m	Dörr & Münnich 1986
Wheat/barley	field/lab	I-^{14}C	75–95	m	Swinnen 1994
Alopecurus/Festuca	field	Cint.	37–60 (0–10 cm layer)	d	Gloser & Tesarova 1978
Salix/Saxifraga	field	Cint.	10 low biomass	d	Nakatsubo et al. 1998
"	field	Cint.	50 high biomass	d	"
Zea	field	I-C4/C3	35–40 growing	d	Rochette & Flanagan 1997
"	field	I-C4/C3	<10 dormant	d	"
Zea	field	I-C4/C3 and Rexcl.	0 at planting	d	Rochette et al. 1999
"			7–12 day 190	d	"
"			25–32 day 200	d	"
"			40–43 days 210–250	d	"
"			5–30 day 280	d	"
"			0–15 day 303	d	"

[1]Cint. = component integration, Rexcl. = root exclusion, and I-xxx are isotopic labeling approachs (with indicated isotope (i.e., ^{14}C, ^{13}C) or C4/C3 indicating a C4 plant grown on a C3 soil).
[2] '—' indicates that the author did not provide sufficient information for the method category to be identified.

Component integration

Component integration involves separation of the constituent soil components contributing to CO_2 efflux (i.e., roots, sieved soil, and litter) followed by measurements of the specific rates of CO_2 efflux from each component part. Rates of all component parts are then multiplied by their respective masses and summed to yield an integrated total of TS_{cer}. Ideally component integration also includes an *in situ* measurement of TS_{cer} for comparison. If the integrated sum of the component parts is in good agreement with measured total TS_{cer}, then the component estimates from the data are considered valid. A common, but less rigorous, variation on the component integration approach is to measure *in situ* TS_{cer} and the litter and root components, but to solve for the other soil heterotrophic activity by subtraction. Edwards and Harrris (1977) used the modified approach and found good agreement between *in situ* TS_{cer} (1065 g C m^{-2} y^{-1}) and component flux integration (984–1042 g C m^{-2} y^{-1}) in a forest ecosystem. The distinguishing feature and potential limitation of the component integration approach is that root specific respiration rates are measured *in vitro*.

Equations describing the component integration measurement approach for estimating RC are as follows:

$$TS_{cer} = (\text{litter rate} * \text{mass}_{litter}) + (\text{root rate} * \text{mass}_{root}) + (\text{soil rate} * \text{mass}_{soil}), \quad (2)$$

$$RC_{ci} = (\text{root rate} * \text{root mass}), \quad (3)$$

$$\%RC_{ci} = RC_{ci}/TS_{cer} * 100, \quad (4)$$

where RC_{ci} is the component integration (ci) derived estimate of RC in units of flux and $\%RC_{ci}$ is the percentage equivalent.

The disadvantage of the component integration approach is the impact of physically separating the component parts of the soil (i.e., litter, roots, mineral soil). Use of the component integration method forces one to deal with measured mass specific rates that may not reflect *in situ* levels. The removal of litter may modify the soil water status of the surface soil and inadvertently impact the contribution of the soil heterotrophs, and disturbance of the root soil interface raises questions about the ability of component integration to adequately capture normal rhizosphere processes. Recent studies (Burton et al. 1997; Qi et al. 1994) have shown that root specific respiration is dependent on soil CO_2 concentrations with rates reduced under higher CO_2 levels. Soil oxygen levels are similarly important (Palta & Nobel 1989). Attempts to measure respiration of isolated roots for the component integration method must be done under O_2 and CO_2 concentrations typical for the soil atmosphere.

Root exclusion

The root exclusion method is any procedure that indirectly estimates RC by measuring soil respiration with and without the presence of roots (i.e., no direct measurements of bare root tissue are made). Equations describing the root exclusion measurement approach for estimating RC are as follows:

$$RC_{excl} = TS_{cer} - TS_{cer} \text{ (without roots)}, \quad (5)$$

$$\%RC_{excl} = [TS_{cer} - TS_{cer} \text{ (without roots)}] / TS_{cer} * 100, \quad (6)$$

Existing root exclusion techniques may be categorized into three broadly defined areas: (1) root removal – roots are removed, soil is placed back in reverse order of removal, and further root growth is prevented by barriers (alternatively, roots may be removed after a series of TS_{cer} measurements), (2) trenching – existing roots are severed by trenching at a plot boundary but not removed, and a barrier is installed to inhibit future root growth, and (3) gap analysis – aboveground vegetation is removed from relatively large areas (e.g., clearcutting in forests) and TS_{cer} measurements in the gap are compared to TS_{cer} data for a forested area. Examples of each root exclusion method follow:

Root removal: Wiant (1967b) used root removal in a 29-year-old mixed forest plantation in Connecticut and determined that RC was between 45 and 66% (Table 1). Roots were removed in June from 0.5 x 0.5 m areas to a depth of 30 cm and soil was returned to each pit. No barriers were used to limit root invasion since the CO_2 efflux measurements were performed only 2 and 4 weeks after root removal. Significant root invasion was unlikely in this short time period. Wiant (1967b) reported that the root exclusion zones were wetter than the soil in the control plot (i.e., 24% versus 18 to 22%) because transpiration was negligible after root removal. A number of studies have shown that soil moisture has a limited impact on TS_{cer} except under extremely high or low moisture conditions (Edwards 1975; Hanson et al. 1993; Thierron & Laudieout 1996).

Edwards (1991) used a variation of the root removal approach in a study of pine seedlings planted in large buried pots. CO_2 efflux was measured for the belowground system, then for the soil pot 2 days after all roots had been removed. Moisture in the soil was maintained near levels existing at the time of harvest by covering the soil with paper over the 2 day equilibration period. They found root contributions ranging from 54 to 78 percent. Since the entire root system was harvested and both soil and roots were weighed, specific respiration rates as well as total respiration of the entire root and soil

system were calculated. Thierron and Laudelout (1996) used an *in vitro* root exclusion technique in an oak-hornbeam forest in Belgium. By inserting a metal sheet horizontally at 10 cm depth under their CO_2 trapping chambers in the field and comparing CO_2 efflux rates with and without a metal sheet, they determined that most CO_2 flux was from the top 10 cm of the soil. They measured rates of CO_2 flux from a 50 g soil sample (with roots removed) collected from the top 10 cm. By determining the bulk density of the soil under their field chambers they extrapolated their laboratory measured rates to the field and, by subtraction, calculated that root respiration was approximately 90 percent of the total. They corrected for effects of disturbance on respiration rates mathematically and established a Q_{10} relationship to adjust for effects of temperature.

The root removal technique has an advantage over trenching in that abnormal amounts of dead roots are not present to contribute to CO_2 production. Root removal also provides a measure of root biomass which is an important variable for comparison with the intact plot following all observations. Further discussion of soil recovery following disturbance associated with root exclusion methods is included at the end of this section.

Trenching: Ewel et al. (1987) used trenching in slash pine plantations in Florida and found RC of 51 and 62% in a 9-y-old and a 29-y-old slash pine stand, respectively. One of the biggest concerns with the trenching approach is the influence of residual decomposing roots left in the trenched plots and their contribution to TS_{cer}. Ewel et al. (1987) addressed this problem by allowing several months to pass after trenching before collecting CO_2 efflux data and by periodically sampling fine root biomass in the trenched plots. They avoided large roots by establishing trenched plots away from the base of tree stems. They also separated the contribution of surface organic matter by removing the litter from some of the plots and replacing it with styrofoam “peanuts”, thus reducing disturbance of the soil boundary layer and any accompanying effects on CO_2 efflux. Bowden et al. (1993) used the trenching technique in an 80-y mixed hardwood forest in Massachusetts and assumed residual root decomposition contributed little to belowground respiration because their measurements began 9 months after the plots were trenched. They cited earlier research showing C content of decomposing fine roots to be relatively stable 4 months after decay began. Bowden et al. (1993) estimated that root respiration contributed 33% to 49% of belowground respiration depending on the contribution of decaying roots. They made a convincing argument that fine root decomposition had little impact on measurements. However, they did not address the issue of large lateral root decomposition which may have been present in the trenched plots. Furthermore, by clipping

at the surface periodically during the summer, Bowden et al. (1993) made sure that new vegetation did not develop in the trenched plots. In some forests more frequent removal of vegetation would be needed to prevent new root development in similar trenched plots.

Gap formation: Brumme (1995) compared soil respiration rates in a mature (146-y-old) beech stand in Germany to rates in 30 m gaps in the stand that had been created 2 years earlier. He measured the lowest rates in the center of the gaps, and found little effect of moisture differences on soil respiration rates. He estimated that living root respiration amounted to about 40% of TS_{cer}. Using a similar technique in a mature deciduous forest in western Japan, Nakane et al. (1996) found root contribution to be about 51% of the total. In the Japan study soil moisture and temperature in the gap plots were maintained equal to that of the forested plots. Temperature was controlled by shading in the gap plots, but it was not clear how moisture was regulated. Herbicides were used to prevent regrowth of vegetation. Because the study was performed soon after clear-felling the problem of root decay might have been greater than in the study of Brumme (1995). In the Japan study about 20% of the CO_2 efflux in the gap was attributed to decay of roots killed by the treatment. Gap studies have some of the same problems as trenching, but with appropriate precautions the technique is attractive in terms of labor, especially if gaps have already been established in the system from individual tree death or windthrow. Clearly, any gap must be large enough that roots from surrounding vegetation are not in the area of measurement, but not big enough to change the physical environment in the soil.

Further discussion of root exclusion techniques

Root exclusion techniques generally result in an initial flush of CO_2 out of the soil following disturbance. Time must pass for the increased CO_2 production rate to subside, and to allow time for the diffusion rates and production rates of CO_2 to come back to equilibrium. For example, Edwards (1991) found that 2 days were required for CO_2 efflux rates to stabilize after pine root removal from soil in large (24 L) pots. Many authors of the previously described methods of obtaining RC data from root exclusion approaches addressed the disturbance problem, but others either ignored it or did not mention how it was handled. Blet-Charaudeau et al. (1990) conducted *in vitro* analyses of the time course of CO_2 evolution from agricultural soils and concluded that much of the initial CO_2 losses following disturbance of the soil were attributable to an acceleration of the decomposition of labile organic matter. Such observations clearly suggest that all root exclusion approaches which disturb the natural soil profile need to allow for re-equilibration to steady

state conditions to minimize the impact of disturbance artifacts. Disturbance concerns can never be completely eliminated, but the rationale used by Ewel et al. (1987) and Bowden et al. (1993) which argue that disturbance impacts become trivial with time seem reasonable for approximate measurements of RC. Root exclusion studies are most useful if the measurements extend through a complete annual cycle, but over such a long period there is the possibility of reinvasion of roots into previously root free zones. A recent application of the *in situ* root exclusion approach to a just completed field study (Edwards & Norby 1999) showed that roots will grow under a portion of the artificial barriers placed in the soil (i.e., the roots entered from below).

Root exclusion approaches based on trenching or gaps would be improved if periodic or post-experiment sampling for residual root density was conducted. Such sampling can help ensure that gaps or barriers provide complete exclusion of root regrowth during experiments.

Root exclusion approaches also share the problem that root severance and/or removal results in increased soil moisture, which can affect decomposition and respiration rates. In some systems (i.e., very dry or very wet sites) and at certain times of the year, differences in moisture between root exclusion zones and intact zones must be taken into account. Since soil temperature also has a strong effect on soil and root respiration, any procedure that might affect soil temperature (e.g. the gap technique) must use appropriate precautions to avoid temperature differences or make adjustments in rates using carefully established Q_{10} relationships.

Isotopic methods

Isotopic methods have an advantage over component integration and root exclusion methods because they allow partitioning of TS_{cer} between root respiration and soil organic matter decomposition *in situ* , and avoid the disturbance effects and the assumption of equilibrium in soil C pools common to the previously discussed methods. The major disadvantage of isotopic methods over component integration and root exclusion methods is the complexity of experimental setup and/or the added difficulty and cost of analytical measurements for radioactive or stable C isotopes. A comprehensive presentation of the application of carbon isotope techniques in environmental studies (including additional detail on methodology) can be found in Coleman and Fry (1991).

Isotopic methods for estimating the relative contribution of root and soil organic matter decomposition to TS_{cer} can be broadly classified as: (1) pulse labelling, (2) repeated pulse labelling, and (3) continuous labelling. Either radioactive carbon-14 (^{14}C) or stable carbon-13 (^{13}C) can be used to trace the

origins of TS_{cer}. Although all of these methods depend to varying degrees on mass balance, the three techniques yield slightly different types of information about plant C allocation and the contribution of root respiration to TS_{cer} (Meharg 1994). Both the choice of an isotope method and the timing of tracer additions can be critical to interpretations of the role of the root in contributing to soil CO_2 efflux.

Pulse labelling and repeated pulse labelling

Pulse labelling is the single addition of a tracer (usually ^{14}C- or ^{13}C-labelled CO_2) for the purpose of quantifying the distribution of labelled C within a plant and the amount of labelled C respired by above and belowground plant parts during a given period of time. Pulse labelling is ideally suited for determining the fate of $^{14}CO_2$ assimilated by small plants grown in closed laboratory chambers where an accounting can be made of all of the ^{14}C added to the system (e.g. Warembourg & Paul 1973; Meharg & Killham 1988; Cheng et al. 1993).

Repeated pulse labelling is a variant of pulse labelling where isotopically labelled CO_2 is administered to plants at different times during the growing season. In some studies, this technique has been used successfully to approximate cumulative plant C budgets (Gregory & Atwell 1991; Jensen 1993; Swinnen et al. 1994a). Pulse labelling repeated at regular intervals has also been used to approximate cumulative belowground C input and rhizodeposition in barley where root respiration was 24% of the total ^{14}C translocated belowground (Jensen 1993). Regardless of whether pulse labelling or repeated pulse labelling is used, there are two critical aspects to the timing of these isotope techniques: (1) chase period and (2) stage of plant growth. These aspects can impose important constraints on the use of pulse labelling methods for estimating root CO_2 flux (Paterson et al. 1997).

The “chase period” is the elapsed time between pulse labelling and the final experimental measurements. The time required for complete allocation of the labelled C within the plant affects the selection of a chase period (Paterson et al. 1997). It is generally assumed that newly assimilated C is quickly translocated throughout the plant. However, there are exceptions depending upon species and stage of plant growth. For example, ^{14}C allocation in wheat plants appears to be completed 19 days after pulse labelling (Swinnen et al. 1994a). The time required for complete allocation does not necessarily correspond to the maximum $^{14}CO_2$ loss rate from the root, which is typically observed within 1 to 7 days after labelling (Horwath et al. 1994; Swinnen et al. 1994a; Xu & Juma 1995). Premature termination of an experiment after isotopic labelling can lead to erroneous conclusions about the significance of shoot and root respiratory losses. This is because plant C pools

most influenced by recently assimilated photosynthate (i.e., nonstructural C pools) are more readily labelled: pulse labelling usually does not result in a homogeneous labelling of plant C pools. For example, it can be expected that sugars, as well as other labile C compounds, will be heavily labelled following ^{14}C pulse labelling (Kuhns & Gjerstad 1991). Differences in the ratio of labile to resistant C compounds can affect root respiration rates in ^{14}C labelled barley plants (Xu & Juma 1995). Pulse labelling may overestimate respiratory losses of labelled C through the root (Meharg & Killham 1988; Kuhns & Gjerstad 1991; Horwath et al. 1994) because labile C compounds in the plant are preferentially labeled. In ryegrass, ^{14}C losses through root respiration following a single pulse labelling was over 30 times greater than such losses from pre-labelled plants where allocation of the ^{14}C label was more complete (Meharg & Killham 1988).

Plant growth stage has also been shown to be critical to estimating root respiratory losses of ^{14}C labelled plants. Depending on the age of the plant, newly assimilated ^{14}C may be allocated primarily to aboveground or belowground biomass (Keith et al. 1986; Gregory & Atwell 1991; Jensen 1993) and lost either through shoot respiration or root respiration. In barley and wheat, young plants labelled with ^{14}C rapidly translocated the ^{14}C to the root systems, but an increasing percentage of ^{14}C was directed to shoots as the plants matured (Gregory & Atwell 1991). Due to changes in C allocation over a growing season, repeated pulse labelling will normally be required to estimate the contribution of root respiration to annual soil CO_2 efflux.

Research by Horwath et al. (1994) exemplifies the effort and difficulty of ^{14}C pulse labelling studies in tree-soil systems. Hybrid poplar trees (>3 m height) were pulse labelled with $^{14}CO_2$ under field conditions in July and September using a large plexiglass chamber (3.2 m height $\times$ 3 m $\times$ 4 m). The root systems of eight individual trees were isolated in 1 m^3 soil blocks using plywood dividers and vinyl sheeting. With the chamber in place, soil CO_2 efflux around each tree was captured by pumping air from the chamber head space through a solution of sodium hydroxide. Soil respiration traps were sampled twice daily and randomly selected trees were harvested two weeks after labelling to determine the distribution of assimilated $^{14}CO_2$. Carbon-14 concentrations in TS_{cer} peaked two days after labelling, but C allocation within the trees did not appear to be complete until two weeks later, when the specific activity of ^{14}C in TS_{cer} was less than 5% of the peak measured value. Based on mass balance, root respiration in July and September accounted for 9 and 12%, respectively, of the ^{14}C recovered and, with further assumptions, it was concluded that root respiration contributed 20% to total soil CO_2 flux over the period of the experiment.

In another study, Edwards et al. (1977) pulse labelled one tree of each of three species (*Liriodendron tulipifera, Pinus echinata*, and *Quercus alba*) under field conditions by stem well injection of ^{14}C-sucrose in early fall. The injected trees were 11 to 16 cm diameter at ~1.4 m. Beginning one week after labelling, TS_{cer} was measured monthly in the vicinity of each tree for 10 months. Large losses of ^{14}C from the root were observed within one week after labelling. The initial losses probably reflected metabolism of labile ^{14}C labelled compounds that were rapidly translocated to the trees' root systems. The flux of $^{14}CO_2$ from the soil surrounding each tree declined and remained low during plant dormancy in the winter months and increased in early summer (May and June). This summer increase was attributed to (1) the release of ^{14}C from carbohydrates stored in roots during the winter and subsequently used for maintenance respiration as soils warmed, and (2) an increase in the sloughing and decomposition of fine roots. This study is one that demonstrates how tracers can be used to describe seasonal trends in the contribution of root respiration to TS_{cer}.

Depending upon the circumstances, calculation of the fractional contribution of root respiration to TS_{cer} can be complex in pulse labelling experiments (Swinnen et al. 1994b). Simple mixing models are usually not applicable following pulse labelling because the labelled C in the plant-soil system is never truly at steady state and the specific activity of ^{14}C (Bq ^{14}C:mg ^{12}C) in root tissues and TS_{cer} is continually changing over time (Warembourg & Paul 1973; Keith et al. 1986; Gregory & Atwell 1991; Horwath et al. 1994). An estimate of the contribution of root respiration to TS_{cer} is theoretically possible if time integrated measures of $^{14}CO_2$ flux and total soil CO_2 flux are available. Usually, a complete accounting of labelled C allocation within the plant is made (e.g., Warembourg & Paul 1973; Keith et al. 1986; Meharg & Killham 1988; Horwath et al. 1994; Swinnen et al. 1994a; Avice et al. 1996) and, root and/or shoot respiration is approximated by the difference between ^{14}C assimilated by the plant and ^{14}C present in biomass and soil at the end of the chase period. Alternatively, the contribution of root respiration to TS_{cer} may be estimated by difference between plant and soil systems where either the plant or the microbial substrate has been labelled by ^{14}C addition (Swinnen et al. 1994b).

Despite its applicability to field situations and apparent simplicity, pulse labelling with $^{14}CO_2$ has important limitations, including issues related to health and safety. The use of ^{14}C at tracer levels (micro- to millicurie amounts) requires measures for the protection of human health and the proper disposal of radioactive wastes. For reasons associated with safety and waste disposal, tracer studies with stable ^{13}C (Avice et al. 1996) are an attractive alternative to the use of tracer ^{14}C for determining plant C allocation, but they

share the same methodological limitations and constraints previously discussed. Although pulse labelling studies are ideal for studying the dynamics of within plant C allocation (Paterson et al. 1997) and the qualitative timing of root respiration (Edwards et al. 1977), they are not well suited to quantification of the contribution of root respiration to TS_{cer} under field conditions. The short-term pulse labelling studies have many advantages with respect to degree of quantification, cost, complexity of setup, difficulty of analysis, and soil-plant disturbance, but they poorly represent the range of pools of C of interest (Figure 1) with respect to the question of root contributions to TS_{cer}.

Continuous labelling approaches

Continuous labelling is accomplished by the assimilation of uniquely labelled C by plants under laboratory (chamber) or field conditions over time periods that are comparable to the life span of a plant. The main advantages of continuous labelling over pulse labelling are: (1) it provides a more homogenous labelling of plant C pools, and (2) steady state assumptions, which simplify calculations, can often be applied. The disadvantages of continuous labelling (Meharg 1994) are: (1) it has poorer time resolution than pulse labelling and therefore is not well suited to the study of transient plant C dynamics, (2) the equipment required for continuous labelling with tracer levels of ^{14}C is expensive and cumbersome making field applications difficult (especially in forest communities), and (3) over time the soil organic matter acquires an isotope signal that is similar to C inputs from the labelled plants making it increasingly difficult to distinguish root respiration and soil organic matter decomposition as separate CO_2 sources.

Laboratory chambers have been used for continuous labelling of small plants with tracer levels of ^{14}C (Warembourg & Paul 1973; Cheshire & Mundie 1990; Liljeroth et al. 1994). Such studies can be instrumental in determining the factors influencing the contribution of root respiration to TS_{cer}. For example, wheat and corn plants continuously exposed to $^{14}CO_2$ exhibit higher rates of rhizodeposition and root respiration at high soil nitrogen levels (Liljeroth et al. 1994). However, chamber experiments with tracer amounts of ^{14}C are not well suited to measurements on larger plants, such as trees. With current methods for measuring small differences in C isotopes (^{14}C, ^{13}C, and ^{12}C), there are fewer reasons why continuous labelling techniques should be confined to studies of small plants using tracer levels of $^{14}CO_2$ in laboratory growth chambers. Obstacles to the field methods of continuous labelling can potentially be overcome through a variety of approaches including (A) the use of bomb derived ^{14}C, (B) the interpretation of changing stable carbon isotopic signatures due to a change in photosynthetic pathway

of the growing plants, and (C) the exposure of plants to unique stable isotopic signatures made possible by large-scale free-air CO_2 enrichment (FACE) experiments.

A. Bomb derived ^{14}C

Nuclear weapons testing during the 1950s and early 1960s increased the ^{14}C content of atmospheric CO_2 (Vogel & Uhlitzsch 1975) and, in effect, created a global long-term labelling experiment that resulted in more uniform labelling of plant and soil C pools than was possible from short-term pulse labeling studies. Dörr and Münnich (1987) suggested that the contribution of root respiration to TS_{cer} can be quantified by measuring the abundance of ^{14}C in atmospheric CO_2, soil organic matter, and soil respiration. Seasonal changes in root respiration and soil organic matter decomposition contribute to annual variation in the ^{14}C content of TS_{cer} (Dörr & Münnich 1986, 1987). The ^{14}C content of CO_2 produced by root respiration can be assumed to reflect its source (atmospheric CO_2) while the CO_2 produced upon decomposition of soil organic matter has a much less modern ^{14}C signature due to its longer turnover time and resulting isolation from the atmospheric bomb ^{14}C. High summertime rates of root respiration cause the ^{14}C content of TS_{cer} to approach that of atmospheric CO_2 (indicating a large fractional contribution of root respiration) while low wintertime rates of root respiration cause the ^{14}C content of TS_{cer} to approach that of CO_2 produced by soil organic matter decomposition (Dörr & Münnich 1986). Dörr and Münnich (1986, 1987) used mass balance calculations, partly based on ^{14}C measurements, to determine that root respiration contributed about 40% to 50% of the total annual soil CO_2 efflux from grass covered and forested soils near Heidelberg, Germany.

B. Stable isotope techniques

Stable isotope techniques for quantification of contributing sources to TS_{cer} are based on a change in photosynthetic pathway (e.g., growing C4 plants on a soil containing organic matter derived from C3 plants) or a long-term change in the ^{13}C abundance in ambient CO_2. Plants with a C3 or a C4 photosynthetic pathway differ in their C isotope composition by approximately 14 ‰ (O'Leary 1988). The average $\delta^{13}C$ value of C3 and C4 plants is –12 and –26 ‰, respectively. Furthermore, there is little evidence for isotopic fractionation during plant respiration (Lin & Ehleringer 1997) and respired CO_2 is assumed to have a $^{13}C/^{12}C$ ratio similar to that of plant tissue. Decomposition of organic matter in soils cropped with C_3 or C_4 plants yields CO_2 that is similar to the photosynthetic pathway contributing to the soil organic matter (Schonwitz et al. 1986).

Robinson and Scrimgeour (1995) used the isotopic difference between the C_3 and C_4 photosynthetic pathways to estimate the contribution of root respiration to soil CO_2 efflux under Bermuda grass. The calculation was based on a linear mixing model with two contributing sources that had different isotopic signatures, and the calculation assumed negligible isotopic fractionation during respiration from C_4 plants and from decomposition of C_3-derived soil organic matter. The fraction of TS_{cer} originating from root respiration (f) is calculated from the following equation:

$$f = (a - c)/(b - c), \tag{7}$$

where a is the ^{13}C abundance in soil CO_2, b is the ^{13}C abundance in CO_2 from root respiration (assumed to be the same as plant C), and c is the ^{13}C abundance in CO_2 from decomposition of soil organic matter (assumed to be the same as that in soil organic matter). With this simple mixing model, the proportion of TS_{cer} originating from decomposition of soil organic matter is 1–f. Bermuda grass (a C4 plant) was grown on a soil containing soil organic matter derived from C3 plants. The $\delta^{13}C$ of soil CO_2 from soil organic matter (without plants) was –20.5 ‰ and that of Bermuda grass was –12.8 ‰. The fractional contribution of root respiration to soil CO_2 flux varied from 40 to 100% over the growing season.

A similar approach to the quantification of root respiration has been undertaken by growing *Zea mays* (a C_4 plant) on soil developed under C_3 vegetation (Rochette & Flanagan 1997; Rochette et al. 1999). Based on the C isotope ratio of soil CO_2 in the *Zea* versus control plots, Rochette and Flanagan (1997) estimated that the root contribution to total soil respiration varied between 5 and 50% over an entire year. The greatest root contribution was during the middle of the growing season. The $\delta^{13}C$ value of soil CO_2 was less negative during C_4 plant growth because of the increasing fractional contribution of root respiration to TS_{cer}. The precision of this technique declines late in the growing season possibly because of CO_2 diffusion into soil caused by gradients in soil temperature (Rochette et al. 1999).

Lin et al. (1998) used a dual-isotope approach involving ^{13}C and ^{18}O isotopic compositions to quantify three components of TS_{cer} in terracosms containing 4-year-old Douglas fir seedlings. In their study, 60 to 64% of TS_{cer} originated from decomposition of soil organic matter and 23 to 32% originated from root respiration. The relative importance of each source varied over the course of the growing season. Lin et al. (1998) present an informative discussion of assumptions and potential errors associated with their dual-isotope approach.

There are several important constraints on using stable C isotopes to measure the contribution of root respiration to TS_{cer}. The principal limitation

is that, in the absence of a change in photosynthetic pathway, the isotopic differences between CO_2 produced by root respiration and CO_2 produced by decomposition of soil organic matter are small relative to existing background isotopic fractiontation. Mary et al. (1992) reported such fractionation during the decomposition of roots, mucilage, and glucose. The CO_2 evolved during decomposition was less enriched in ^{13}C than the substrate and the extent of fractionation varied depending upon the stage of decomposition. In addition, isotopic fractionation can bias calculations of contributing sources to TS_{cer} based on linear mixing models. Carbon dioxide produced in the soil is more enriched in ^{13}C than the CO_2 flux at the soil surface. Soil CO_2 is about 4‰ more enriched in ^{13}C than CO_2 in TS_{cer} due to fractionation associated with diffusion as $^{12}CO_2$ diffuses to the soil surface faster than $^{13}CO_2$ (Dörr & Münnich 1980; Cerling et al. 1991). Therefore, a distinction must be made between the isotope composition of TS_{cer} and soil CO_2. Because $\delta^{13}C$ values of soil CO_2 often vary with soil depth (Cerling et al. 1991), soil CO_2 for isotope analysis is usually sampled from buried gas sampling tubes within the soil profile (Cerling et al. 1991; Hesterberg & Siegenthaler 1991; Robinson & Scrimgeour 1995). Small changes in atmospheric pressure over the course of a day may force diffusion of atmospheric CO_2 (–8 ‰) into the soil which will affect the isotopic composition of soil CO_2 and complicate the interpretation of contributing sources to TS_{cer} (Dudziak & Halas 1996b).

C. FACE experiments

Free air CO_2 enrichment (FACE) experiments provide the opportunity to add a ^{13}C label to an intact ecosystem continuously. A circular FACE plot (Lewin et al. 1992) is surrounded by a series of vertical vent pipes that fumigate vegetation with CO_2, maintaining an elevated concentration without the use of enclosures. While the main purpose of a FACE experiment is to examine the effects of high atmospheric CO_2 on plant and ecosystem processes, a consistent and distinct ^{13}C label in the fumigation gas can provide a means by which root-derived CO_2 can be separated from TS_{cer}.

This technique has been applied at the FACE experiment located in a 15-year-old loblolly pine plantation at Duke University (Ellsworth et al. 1998). The fumigation CO_2 is derived from natural gas, and is strongly depleted in ^{13}C ($\delta^{13}C$ = –39.3 ‰) relative to the ambient atmosphere ($\delta^{13}C$ = –8 ‰). Elevation of the Duke-FACE atmosphere by 200 ppm changed the plot CO_2 $\delta^{13}C$ from –8 to –21 ‰. The additional photosynthetic fractionation in the loblolly pine, approximately –20 ‰, resulted in new photosynthate with $\delta^{13}C$ = –41 ‰, which is respired by the roots. The relative contribution of the root to soil respiration can be calculated by assuming that the CO_2 produced by soil heterotrophs has the isotopic signature of the soil under nonfumigated forest

and that all of the labeled CO_2 is derived from root respiration. Considering the addition of the ^{13}C label to the SOM pool after one year of fumigation, the contribution of root respiration can be calculated with another form of equation 7 where f is the fraction of soil respired CO_2 from roots, a is the $\delta^{13}C$ of soil respired CO_2 under FACE (–33.2 ‰), c is the $\delta^{13}C$ of heterotroph respired CO_2 as measured from root-free soil incubations (–25.7 ‰), and b is the $\delta^{13}C$ of root respired CO_2 (–39.3 ‰). Using these early September observations from the Duke FACE study, roots were shown to contribute 55% of total soil respiration (Jeff Andrews, unpublished data).

The continuous labeling technique as applied in a FACE experiment also has important limitations. For instance, the assumption of a unique root-derived label fails as the ^{13}C signal moves into other soil C pools. In the Duke FACE experiment, the incorporation of the ^{13}C label to the extremely labile SOM pool, presumably through root exudates, occurred within a year of the start of fumigation, as determined from root-free soil incubations. This ^{13}C signal, if not considered in calculations of root respiration, will cause an over-estimation of the root CO_2 contribution. As labeled aboveground litter is added to the soil surface (Figure 1), decomposition in the organic soil horizons will result in an additional depletion of the soil respired CO_2 $\delta^{13}C$ signal.

Ultimately, this continuous labeling technique is also limited by the response of plants to FACE. As the distinctive ^{13}C label is added to the FACE plot, the CO_2 fertilization effect may increase root respiration (Schlesinger & Andrews 1999). Over the life-time of these experiments, FACE projects may give us a better understanding of the relative contribution of root respiration under future CO_2 conditions than they do about the current partitioning of soil respiration.

Published estimates of root contributions to FF_{cer}

We found 50 studies in the literature that either made an estimate of root contribution to total TS_{cer} or had sufficient data from which we could make our own estimate (Table 1). Surprisingly, two papers commonly cited as a reference for quantitative information on root contribution to total TS_{cer} (Odum & Jordan 1970; Witkamp & Frank 1969) contained no direct data that could be interpreted for inclusion in Table 1. Of the studies in Table 1, 37 were for forests and 14 were for grassland or crop systems. A comprehensive search for data from crop studies was not attempted and additional observations may be available.

A histogram of all reported data (Figure 2(a)) shows the modal RC to lie in a range from 40 to 50% with an overall mean RC of 48%. Especially low

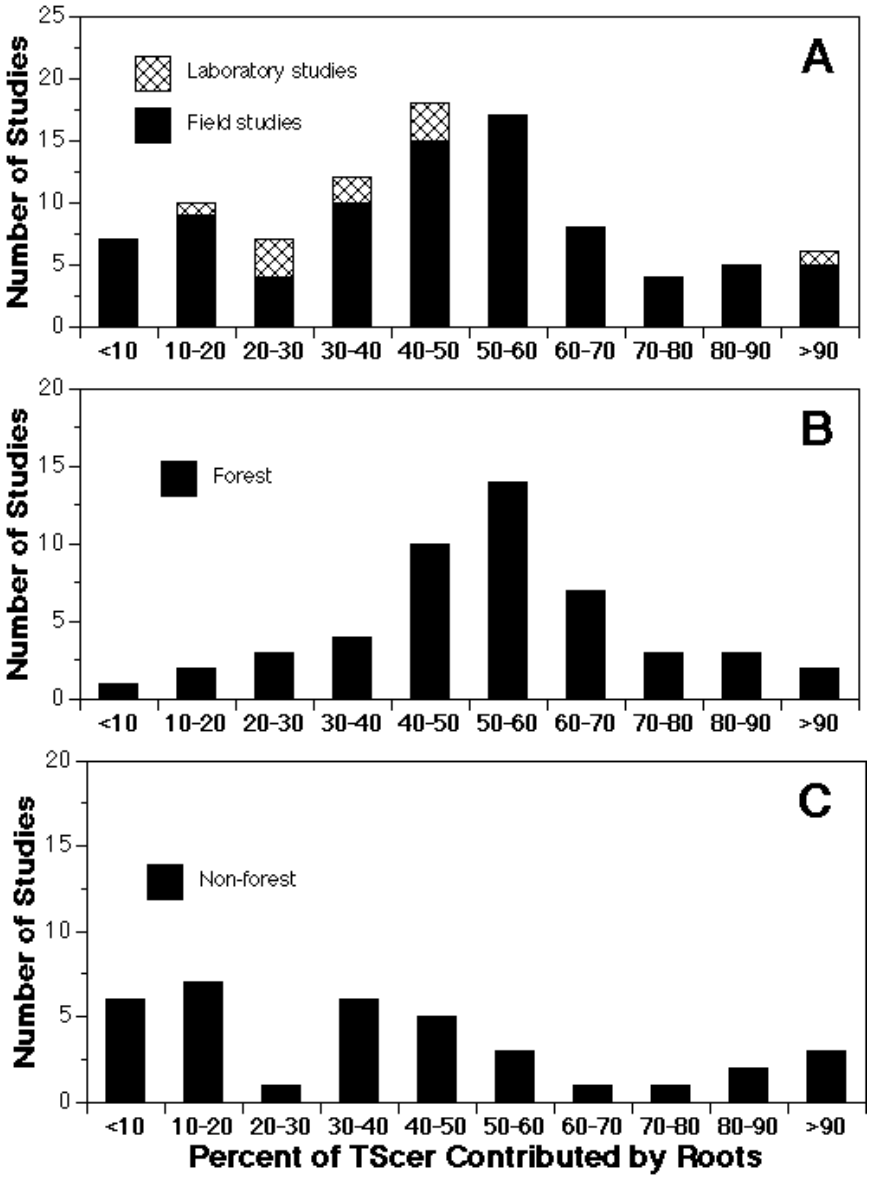

Figure 2. Histograms of the percent root contribution to TS_{cer} for all laboratory and field based studies (A) and separate graphs for forest (B) and nonforest studies (C). The laboratory-based observations were not included in graphs B and C. Measurement periods vary among compiled studies (see Table 1).

values of RC (i.e., <20%) were more common among non-forest observations (Figure 2c). Low RC values reported for *Quercus* forests and old fields by Coleman (1973) were based only on the upper 5 cm of the soil profile and therefore are most likely underestimates of the total RC. The estimated RC for specific soil horizons provided in several papers (Uchida et al. 1998; Flanagan & Van Cleve 1977; Hendrickson & Robinson 1984) was included in Table 1, but it was not added to the histograms of Figure 2.

Field based forest and nonforest data sets are plotted separately in Figures 2b and 2c. RC for sites dominated by forest vegetation averaged 48.6% and the data exhibit a normal distribution. The RC values for the nonforest vegetation is spread throughout the entire range with an overall average of 36.7%. The conclusion of a mean RC near 50 percent differs substantially from the prior estimate of RC used by Raich and Schlesinger (1992) in their global analysis of the impact of warming on soil respiration and soil carbon turnover rates. Had Raich and Schlesinger used a value of RC closer to the 50% value supported by the data in Table 1 their estimate of total soil carbon turnover times would have been changed. Larger values of RC imply lower values of heterotrophic respiration. Reduced rates of heterotrophic respiration in the analysis provided by Raich and Schlesinger (1992) would have increased their estimates of the soil turnover time for an average forest ecosystem. The true nature of RC must be identified before analysis of TS_{cer} data can be interpreted with respect to soil carbon storage.

Although most studies in Table 1 deal with estimates made during the middle of the growing season, a number of the studies contrasted growing versus dormant season RC (Minderman & Vulto 1973; Dörr & Münnch 1986; Edwards 1991; Rochette & Flanagan 1997). These studies found much lower RC during the dormant season. Root respiration is dependent on short term changes in the supply of carbohydrates from plant shoots (Huck et al. 1962; Osman 1971), and Johnson-Flanagan and Owens (1986) have shown that root respiration is also controlled by morphological and internal metabolic changes. Hanson et al. (1993) provide evidence which shows that the contribution of roots to TS_{cer} can change dramatically throughout an annual cycle in conjunction with CO_2 evolution associated with root construction costs. Edwards et al. (1977) directly measured the seasonal patterns of $^{14}CO_2$ efflux from the roots of a white oak tree and found that the rate of root-derived CO_2 efflux increased dramatically during the May–June period. Work from Tennessee hardwood forests (Edwards & Harris 1977) and Missouri white oak forests (Joslin 1983) has also shown that the time period from mid-May through June is characterized by high root growth and root turnover. The implication of the importance of root construction costs to seasonal changes

in TS_{cer} is that we should not attempt to use a single value of RC as we integrate short term TS_{cer} data throughout annual cycles.

The data in Table 1 can also be evaluated according to the time period over which a particular study measured RC (i.e., days, weeks, months, or a year). Such a breakdown yields similar values among time periods for forests, but quite different RC data among time periods for nonforest vegetation. Forest data integrated annually, monthly, and daily yielded a mean RC of 45.8, 50.4, and 55.6%, respectively. The nonforest data were very different showing mean RC values of 60.4, 62.6, and 20.3%, respectively for the annual, monthly, and daily studies. The reduced estimate of RC for nonforest sites measured daily may be the result of the estimates from old field (Coleman 1973) and crop studies (Rochette et al. 1999; Rochette & Flanagan 1997) where root density below ground is lower than for untilled sites dominated by natural vegetation.

Recommendations and conclusions

Comparative studies of component integration, root exclusion, and isotopic approaches for separating root respiration from total TS_{cer} are sorely needed, but unfortunately very rare. One recent example of such a methods intercomparison was conducted on maize plants by Rochette et al. (1999). They found that the ^{13}C isotopic labeling and root exclusion methods produced similar values for RC, and concluded that both approaches were useful. The paucity of similar studies limits rigorous evaluation of the precision and accuracy of the various approaches presented in this paper, but a number of conclusions regarding the relative merit of each method can be drawn.

1. Stable isotope techniques based on changing photosynthetic pathways hold considerable promise for assessing the contribution of root and soil organic matter decomposition to TS_{cer}, because they involve less disturbance to the soil-plant system than root exclusion or component integration techniques. However, there are uncertainties about how quantitative these methodologies are when used in the field.
2. Stable isotopic approaches which use overplanting of C_4 plants on C_3 soils is an increasingly popular method of estimating RC. Unfortunately, it is difficult to find situations where forests (C_3 plants) are growing on soils containing soil organic matter derived from C_4 plants. Nonetheless, this approach may be appropriate for reforestation studies on croplands previously under long term C_4 plant cultivation.
3. The bomb-^{14}C method may be the best for distinguishing the various sources of CO_2 contributing to TS_{cer} in extant forest ecosystems, but the

difficulty and cost of analysis will likely limit the use of bomb-^{14}C as a routine tool for analysis of RC.

4. Isotope approaches have a clear advantage over other methods because they limit soil and root disturbance, but this advantage comes at a substantial increase in cost and complexity of the analyses.
5. In situations where high costs and/or the lack of appropriate expertise might limit the use of isotope approaches, future investigators might consider the root exclusion techniques which have been shown to produce comparable RC data (Rochette et al. 1999).
6. Regardless of the method selected, future studies of RC must involve repeated measurements throughout an annual cycle to adequately characterize seasonal variation driven by changing patterns of below ground root activity.

Future attention to the contribution of roots and rhizosphere organisms to TS_{cer} will be required if short-term measurements of TS_{cer} are to be used to evaluate net C exchange from forest soils (Equation 1). New observations of RC collected simultaneously with repeated TS_{cer}measurements distributed throughout entire annual cycles will further our understanding of soil carbon cycling and sequestration, and provide valuable input to the discussions of soils as potential sinks for atmospheric carbon dioxide.

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