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Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements

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Abstract

Allocation of C to belowground plant structures is one of the most important, yet least well quantified fluxes of C in terrestrial ecosystems. In a literature review of mature forests worldwide, Raich and Nadelhoffer (1989) suggested that total belowground carbon allocation (TBCA) could be estimated from the difference between annual rates of soil respiration and aboveground litterfall. Here we analyze new measurements of soil respiration and litterfall, including data from the Ameriflux network. Our results generally agree with Raich and Nadelhoffer's previous work. A regression analysis of data from mature forests produced the following relationship: annual soil respiration $= 287 + 2.80 \times$ annual litterfall. This regression slope indicates that, on average, soil respiration is roughly three times aboveground litterfall-C, which further implies that TBCA is roughly twice annual aboveground litterfall-C. These inferences are based on the uncertain assumption of soil C stocks being at steady state. Nevertheless, changes in soil C would have to be very large to modify the conclusion that TBCA is generally much larger than litterfall. Among only mature temperate hardwood forests, however, the correlation between litterfall and soil respiration was poor, and the correlation among years for a single site was also poor. Therefore, the regression cannot be relied upon to provide accurate estimates of soil respiration or TBCA for individual sites. Moreover, interannual variation in TBCA, short-term changes in C stocks, or different temporal scales controlling leaf litter production and soil respiration may cause important deviations from the global average. The regression slope for data from young forests is steeper, possibly indicating proportionally greater TBCA, but the steady-state assumption is more problematic for young forests. This method

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for estimating TBCA may be most appropriate where interannual variation is averaged over several years of observations and where a near-steady-state assumption of soil, litter, and root C stocks is least problematic.

Keywords: Carbon dioxide (CO_2); Carbon cycling; Forest ecosystems; Forest soil; Infrared gas analyzers; Roots; Soil carbon

1. Introduction

Allocation of C to belowground plant structures often equals or exceeds aboveground litterfall-C and aboveground respiration in forest ecosystems, making it the single most important fate for gross primary productivity (Janssens, 2001). Despite its importance, total belowground carbon allocation (TBCA) remains poorly quantified because it is difficult to quantify root and mycorrhizal processes by any method (Hanson et al., 2000; Hendrick and Pregitzer, 1993; Kurtz and Kimmons, 1987; McClaugherty et al., 1982; Zak and Pregitzer, 1998). In the absence of direct measurements of TBCA, Raich and Nadelhoffer (1989) proposed that the difference between soil respiration (Rsoil) and litterfall-C could be used to estimate TBCA in ecosystems where the stocks of soil organic matter, roots, and litter were assumed to be near steady state:

$$\text{TBCA} = \text{Rsoil} - \text{litterfall-C} \quad (1)$$

Using published studies of sites that presumably satisfied the near-steady-state assumption, and assuming that interannual variations in soil and forest floor C stocks are small, Raich and Nadelhoffer (1989) developed a regression formula that related measurements of litterfall and soil respiration. Their correlation based on data from forested ecosystems throughout the world showed TBCA to be about twice litterfall-C.

With the proliferation of whole-ecosystem studies of C balance in the Ameriflux and Euroflux networks (Baldocchi et al., 2001) and complimentary measurements of litterfall and soil respiration, a new opportunity has arisen to evaluate the original review of the Raich and Nadelhoffer (1989) approach. Infrared gas analyzers (IRGAs) are now more commonly used for chamber-based measurements of soil respiration, thus obviating some of the doubts that Raich and Nadelhoffer (1989) had about the quality of data from soda lime techniques that were most common in the literature at that time. The objective of this paper is to re-evaluate the approach for estimating TBCA from measurements of litterfall and soil respiration, using recent results of the Ameriflux network, in addition to several published papers from the Euroflux network and other forests of the world. To avoid methodological inconsistencies that could confound results, only IRGA-based soil respiration measurements made since the Raich and Nadelhoffer (1989) publication are used.

2. Assumptions of the conceptual model of TBCA

Soil respiration (Rsoil) is CO_2 flux from the soil-litter surface and is comprised of root respiration (Rroot), microbial decomposition of soil organic matter derived from dead roots, root exudates, and mycorrhizal hyphae (lumped here as "root litter C decomposition"), and microbial decomposition of aboveground leaf and woody litter:

$$\text{Rsoil} = \text{Rroot} + \text{root litter C decomposition} + \text{aboveground litter C decomposition} \quad (2)$$

A critical assumption of this approach to estimate TBCA is that the root biomass stocks, the litter layer, and mineral soil layers of organic carbon are at steady state. The inputs to these C pools from net primary production equals the amount of decomposition when the stocks are at steady state. When this steady-state assumption is met, so that the annual inputs of C belowground via root exudates, root sloughing, and root and mycorrhizae mortality are equal to annual rates of decomposition of dead roots and root-derived soil organic matter, then the first two terms on the right side of Eq. (2) sum to the total amount of carbon allocated belowground (TBCA), which is expressed in Eq. (3):

$$\text{TBCA} = \text{Rroot} + \text{root litter C decomposition} \quad (3)$$

Similarly, the amount of annual litterfall equals the amount of decomposition of the aboveground litter

when the litter layer is at steady state:

$$\text{aboveground litter C decomposition} = \text{litterfall-C} \quad (4)$$

Raich and Nadelhoffer (1989) point out that the steady-state assumption need not be absolutely correct, but that the annual changes in the soil and litter stocks must be small relative to soil respiration and litterfall-C. For example, Gaudinski et al. (2000) used radiocarbon measurements to estimate that the upper limit of soil C sequestration at the Harvard forest in Massachusetts is about 30 g C m^{-2} per year, whereas Savage and Davidson (2001) report 5-year averages of 750 g C m^{-2} per year soil respiration and 220 g C m^{-2} per year litterfall in the same forest. Hence, although we cannot be confident that the Harvard forest soil-C is exactly at steady state, the magnitude of the gain in soil C is likely to be <4 and <14% of soil respiration and litterfall, respectively. When the changes in C stocks are small relative to soil respiration and litterfall fluxes, then the only two terms that make significant contributions to soil respiration are litterfall and TBCA. Substituting Eqs. (3) and (4) into Eq. (2), the following is derived:

$$\text{Rsoil} = \text{TBCA} + \text{litterfall-C} \quad (5)$$

Rearranging Eq. (5) then yields Eq. (1), which estimates TBCA based on measurements of annual rates of soil respiration and litterfall (Raich and Nadelhoffer, 1989).

3. Compilation of datasets

For this analysis, concurrent annual estimates of soil respiration and fine litterfall were needed from each forest site. Several such papers were found in the literature, and several more datasets were offered by participants of a workshop of Ameriflux participants held at Pellston, MI, 4–7 May 2000. We relied upon each investigator to determine his or her best method for annual estimates, which were usually made either from interpolating between measurement dates or from parameterized temperature-dependent models. It should be noted that the data in Table 1 cited as "pers. commun." or those that correspond to the references containing "submitted for publication" in the reference list have not gone through peer review and publication, but to the best of our knowledge, these preliminary results are accurate. Descriptions of the Ameriflux sites are archived at the web site: http://cdiac.esd.ornl.gov/programs/ameriflux/.

Because some sites approach the near steady-state assumption and some do not, we divided the data into two groups: (1) "mature" sites that have not undergone obvious major disturbance during the last 45 years; and (2) "young" sites that were clearly recovering from relatively recent (<45 years) disturbance. Although some mature sites are accumulating carbon (Goulden et al., 1996; Hollinger et al., 1999; Law et al., 2000), most of the C accumulation is probably in the aboveground live and dead biomass and not the soil (Gaudinski et al., 2000). The mean residence time of actively cycling C in the soil is on the order of a few decades (Trumbore, 2000). Therefore, soil C stocks in forest stands that have not undergone major disturbance during the last several decades are likely approaching a steady-state condition. We recognize that changing climate, N deposition, CO_2 fertilization, and successional status may be violating the steady-state assumption, but changes in soil C stocks due to these processes would have to be large relative to annual rates of litterfall and soil respiration to affect the TBCA calculation. We assume that Eq. (1) applies for the mature sites of this study.

For the Ameriflux sites, total fine litterfall is defined as all non-woody material that falls into litterfall traps, including leaves, acorns, fruits, flowers, etc. and woody material that is entirely within the trap, shorter than 20 cm, and with a maximum diameter <1 cm. Unfortunately, not all publications provide specific definitions for their litterfall collections.

Comparisons of regression equations between young and mature forests and between mature forests of this study and of the Raich and Nadelhoffer (1989) study were made using the dummy variable method described by Zar (1996).

4. Results and discussion

4.1. Mature forests

When the data from both young and mature forests are plotted together (Fig. 1), the least squares regression line has a steeper slope (3.61 ± 0.78, 95% CI) than the slope (2.92) reported by Raich and

Table 1
Soil respiration and litterfall data used in this analysis

Sites	Forest description	Plot description	Annual soil respiration ($g C m^{-2}$ per year)	Annual litterfall ($g C m^{-2}$ per year)	References	Plotting symbol
Bavaria, Germany	Norway spruce, 47 years		710	203	Buchmann (2000)	Bv
Cheas, Wisconsin	Mixed northern hardwood, 80 years		945	182	Bolstad (pers. commun.)	Wi
Craigieburn forest park, New Zealand	Nothofagus forests	10-year-old stand, flat	1160	141	Scott (pers. commun.)	NZ1
		25-year-old stand, steep	830	203	Allen et al. (1997)	NZ2
		120-year-old stand, flat	1140	223		NZ3
		150-year-old stand, steep	830	271		NZ4
Duke forest, North Carolina	Loblolly pine forest mixed deciduous, pine <20 years		994	257	Andrews and Schlesinger (2001) and Finzi et al. (2001)	NC
Harvard forest, Massachusetts	Mixed hardwood, 60–100 years	19th century pasture	748	219	Savage and Davidson (2001, pers. commun.)	Ma1
		19th century farm	679	181		Ma2
		19th century logged	647	188		Ma3
Pepeekeo, Hawaii	*Eucalyptus saligna* New plantation growth	Fertilized plot	2150	470	Giardina and Ryan (2002)	Hi1
		Control	1920	380		Hi2
		Densely forested	2200	370		Hi3
		Sparsely forested	1930	460		Hi4
Hesse forest, France	30-year beech forest		619	131	Granier et al. (2000)	Fr
Howland forest, Maine	Old growth spruce with some pine and hardwoods, ~100 years		753	158	Savage and Davidson (2001)	Me
Morgan Monroe State forest, Indiana	Mixed hardwood, 60–80 years		1050	240	Ehman et al. (2002)	In
La Selva, Costa Rica	Tropical evergreen, old growth	Inceptisol	1110	389	Clark et al. (pers. commun.)	CR1
		Ultisol	1480	475		CR2
Northern Michigan Biological Station	Aspen hardwood, 90 years		1160	148	Curtis et al. (2002)	Mi
Oak Ridge, Walker Branch, Tennessee	Mixed hardwood, 50–100 years	Valleys	736	139	Hanson et al. (1993, pers. commun.)	Tn1
		NE slope	818	176		Tn2
		SW slope	846	212		Tn3
		Ridges	927	179		Tn4

Metolius, Oregon	Old growth ponderosa pine (250 years) with patches of 45-year-old trees	Semi-arid, open canopy, pumice soils	780	132	Law et al. (2000, 2001)	Or1
	Ponderosa pine 14 years after clearcut of old growth	Pumice soils, open canopy	654	52		Or2
Paragominas, Brazil	Tropical evergreen old growth		2000	480	Davidson et al. (2000)	Br1
	20-year-old secondary forest		1800	475		Br2
Santarem, Brazil	Tropical evergreen old growth		1700	360	Davidson (pers. commun.)	Br3
Pradas and Montseny, Spain	Oak forest, 40 years	Upper slope, Pradas	291	114	Piñol et al. (1995)	Sp1
		Lower slope, Montseny	197	100		Sp2
Vielsalm, Belgium	Beech subplot	27 m tall, no age given	870	158	Longdoz et al. (2000)	Be1
	Douglas-fir subplot	35 m tall, no age given	438	69		Be2
Zealand Island, Denmark	80-year-old beech		600	235	Pilegaard et al. (2001) and Pilegaard (pers. commun.)	Dk

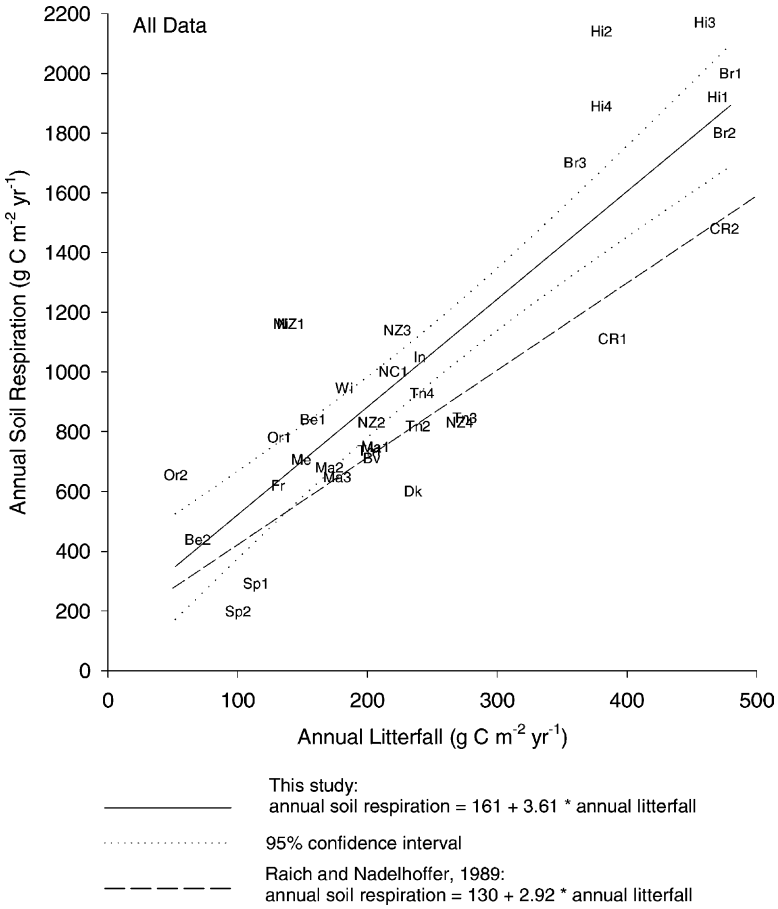

Fig. 1. Regression of annual soil respiration and annual aboveground litterfall-C for all sites shown in Table 1 (see table for identification of plotting symbols). For this study, the regression is significant ($\alpha < 0.01$; $R^2 = 0.73$). The Raich and Nadelhoffer (1989) regression equation is also shown for comparison.

Nadelhoffer (1989), although these slopes are not significantly different. When only mature forests are used in the regression, the slope (2.80 ± 0.98, 95% CI) is similar to the 2.92 slope reported by Raich and Nadelhoffer (1989). Statistical tests showed no significant difference in slopes ($p = 0.77$) or intercepts ($p = 0.20$), although a test of coincidence indicates that the two lines are not coincident ($p = 0.04$; Zar, 1996). This situation occasionally occurs because the test of coincidence has greater statistical power due to more degrees of freedom in the *F*-test than do the tests for intercepts or slopes alone. The *Y*-intercept in this study (287 ± 254, 95% CI) is significantly different from zero, which was not the case for the *Y*-intercept of 130 reported by Raich and Nadelhoffer (1989). In any case, the two regression lines are nearly parallel, but slightly offset (Fig. 2).

Three of the soil respiration rates shown in Fig. 2 for tropical rainforests (CR2, Br1, and Br3) exceed the range reported by Raich and Nadelhoffer (1989). About half of the data points fall very near the Raich and Nadelhoffer regression line and the other half are above this line, indicating that there is a general bias towards higher respiration rates in this study than reported by Raich and Nadelhoffer (1989). Underestimation of soil respiration by the soda lime method (Ewel et al., 1987) used in the majority of studies cited by Raich and Nadelhoffer (1989) may have caused

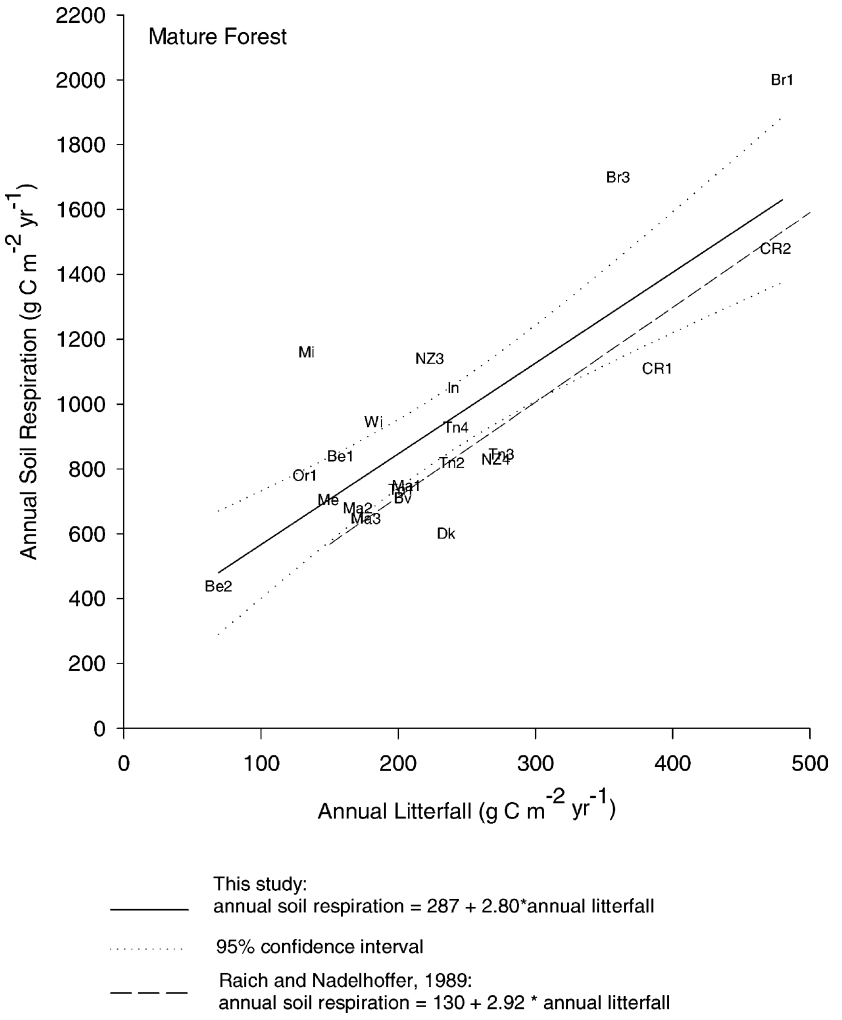

Fig. 2. Regression of annual soil respiration and annual aboveground litterfall-C for all mature forests (45 years of age). See Table 1 for identification of plotting symbols. For this study, the regression is significant ($\alpha < 0.01$; $R^2 = 0.62$). The Raich and Nadelhoffer (1989) regression equation is also shown for comparison.

underestimation of the *Y*-intercept in their regression analysis.

The forest sites in the Brazilian eastern Amazon region (plotted as "Br1" and "Br3") fall above both regression lines (Fig. 2), indicating higher soil respiration than would be predicted from litterfall rates and the regression equations. This region experiences a long dry season, and the canopy is maintained evergreen through uptake of stored soil water by a large and deep root biomass (Nepstad et al., 1994). Hence, it is not surprising that TBCA is above average for these sites. In contrast, the La Selva forest of Costa Rica (plotted as "CR1" and "CR2") receives twice as much mean annual rainfall as the eastern Amazonian sites, experiences only a very brief and mild dry season, and appears to allocate less C belowground relative to its litterfall-C compared to the Amazonian sites.

Given the paucity of sites in this dataset with litterfall >250 g C m^{-2} per year, this regression result must be interpreted with caution. Likewise, not all forest biomes of the world are represented in this dataset; boreal forests are conspicuously absent, and

significant respiration of mosses on the forest floor of boreal forests would complicate and perhaps preclude this approach to estimating TBCA. As in all cross-site comparisons, there could be unidentified differences in definitions of fine litterfall and biases caused by differences in designs of litterfall traps, soil respiration chambers, and spatial and temporal sampling schemes. However, it appears that the results generally confirm the conclusion of Raich and Nadelhoffer (1989), that, on average, annual soil respiration is about three times litterfall-C (more than three times where litterfall is low so that the *Y*-intercept becomes more important). By difference, TBCA is inferred to be about twice (or more) that of litterfall-C. Not surprisingly, however, the global average does not accurately predict TBCA for each specific site, which has also been demonstrated previously (Gower et al., 1996).

4.2. Young forests

The regression equations for the mature and young subsets of data (Figs. 2 and 3) are statistically not coincident ($p = 0.04$), with no difference in intercepts ($p = 0.38$) and a nearly significant difference in slopes ($p = 0.06$). The slope for the young forests (4.16 ± 1.22, 95% CI) is steeper than the slope for the mature forest (2.80 ± 0.98, 95% CI), possibly indicating a larger amount of root respiration or decomposition of root litter contributing to higher soil respiration relative to decomposition of aboveground litter. Although only a marginally statistically significant difference, this trend is consistent with greater investment in belowground C by young forests to establish and maintain a root system capable of supporting the demands for water and nutrients of the

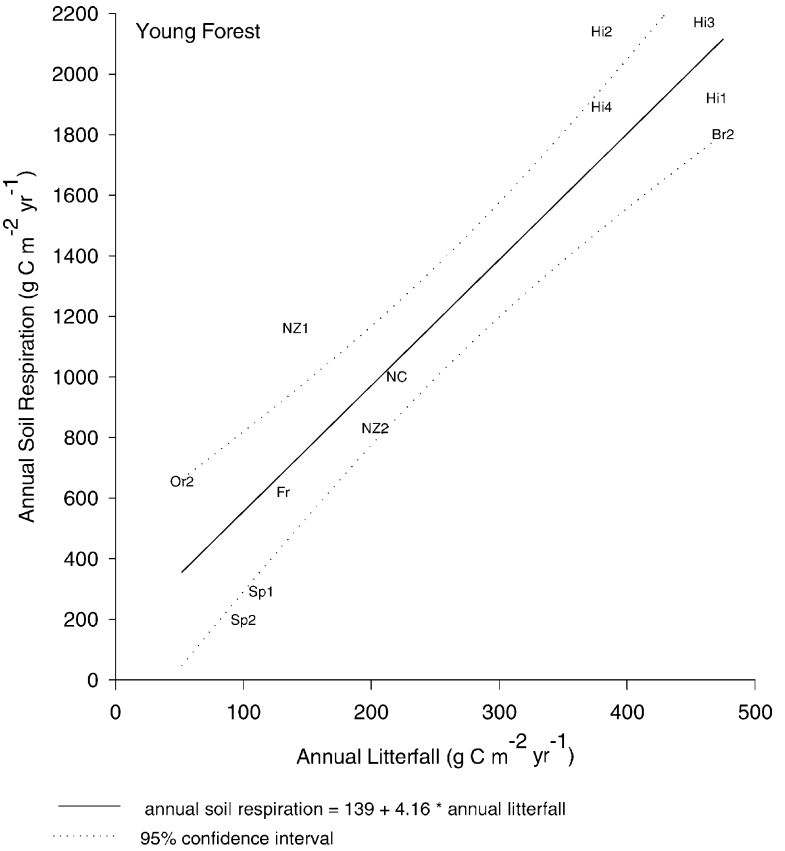

Fig. 3. Regression of annual soil respiration and annual aboveground litterfall-C for all young forests (<45 years of age). See Table 1 for identification of plotting symbols. The regression is significant ($\alpha < 0.01$; $R^2 = 0.81$).

rapidly growing trees (Gholz et al., 1986; Jipp et al., 1998). If root biomass also is aggrading in these sites, then TBCA could be further underestimated by the regression shown in Fig. 3.

Where the assumption of near-steady-state C pool sizes is not applicable, as in young aggrading forests or old, disturbed, or diseased declining forests, Nadelhoffer et al. (1998) have shown that additional terms are needed in this mass balance approach:

$$\text{TBCA} = \text{Rsoil} - \text{litterfallC} + \Delta\text{litterC} + \Delta\text{soilC} + \Delta\text{rootC} + \text{export} \quad (6)$$

where ΔsoilC, ΔlitterC, and ΔrootC are the changes in C stocks of mineral soils, forest floor, and root biomass, respectively, and export is C loss via leaching. When the forest floor is accumulating, litterfall is no longer a good estimate of CO_2 production from decomposition of litter C (Eq. (4)). Likewise, if aboveground litter and/or root litter are being incorporated into soil organic matter (SOM) in a non-steady-state manner, or if there is significant soil erosion, then the ΔsoilC term in Eq. (6) may become important. Leaching of DOC from litter or SOM also violates Eqs. (3) and (4), so that not all of the litterfall-C should be subtracted from soil respiration to estimate TBCA. Finally, coarse woody debris is not included in the fine litterfall estimate, and it is usually avoided in soil respiration measurements, but it could contribute significantly to soil C inputs, particularly in old or disturbed forests.

We do not attempt to estimate the additional terms in Eq. (6) for the "young" sites. These are site-specific parameterizations that are left to site-specific publications. Rather, we point out, as Nadelhoffer et al. (1998) and Gower et al. (1996) have done, that the regressions based on "mature" forests with a steady-state assumption should not be applied to relatively young, aggrading forests.

4.3. Mature temperate hardwood forests

Temperate hardwood forests are the best represented group in this dataset, and we use this group to evaluate variability of TBCA estimates within a single biome. The range of soil respiration and litterfall rates among the temperate hardwood forests is relatively small, and the regression is not significant (Fig. 4; slope $= 1.13 \pm 2.55$, 95% CI). As was the case for the tropical forests already discussed, differences in aboveground and belowground C allocation may vary among the mature temperate hardwood forests, depending on climate, land use history, life history traits of the dominant plant species, and soil type. These results suggests that predicting TBCA from litterfall data, using either the Raich and Nadelhoffer (1989) equation or the one in Fig. 2, may be acceptable for global scale modeling and for obtaining rough estimates, but may not always provide reliable estimates for individual sites (Gower et al., 1996). In other words, the 1:2 ratio of aboveground litter to belowground allocation of C implied by the Raich and Nadelhoffer equation may be roughly correct as a broad-brush approximation, but it is not universal, even among forests near steady state. Indeed, we may learn the most about C allocation by observing how and perhaps why various ecosystems diverge from the "average" 1:2 allocation ratio.

The Michigan site, for example, was included in the regression analysis for mature forests shown in Fig. 2 ("Mi"), but it stands out as having unusually high soil respiration for the amount of litterfall. This mid-successional forest could be unusual because it is currently undergoing a transition from an even-aged aspen stand to an uneven-aged oak forest, which could cause changes in root and soil stocks of C or changes in TBCA. On the other hand, the reported data are for only 1 year, and means of multiple years of data might show that this site conforms to the expected regression predictions. Ongoing measurements will determine whether this site has above average TBCA, or changing stocks of soil and root C, or if the first year's data simply reflect unusual conditions of either soil respiration or litterfall. Although it was not identified as an outlier by the studentized residual, when this point is removed from the regression for mature forests, the slope increases to 3.04, the intercept decreases to 204, and the R^2 value increase from 0.62 to 0.71.

4.4. Interannual variation

One of the uncertainties of using this approach to estimate TBCA is the possibility of interannual variation of either litterfall or soil respiration. The approach implicitly assumes that the controls of soil respiration and aboveground litter production operate

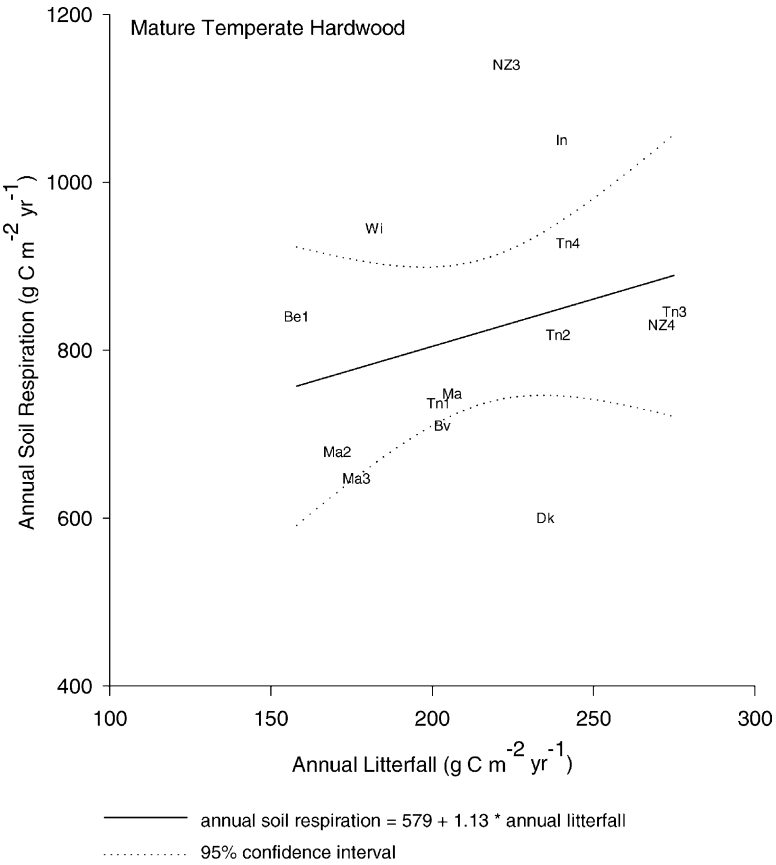

Fig. 4. Regression of annual soil respiration and annual aboveground litterfall-C for mature temperate forests. See Table 1 for identification of plotting symbols. The regression is not significant ($\alpha > 0.05$; $R^2 < 0.01$).

on the same temporal scale. The datasets used here included some cases where these measurements were averaged over more than 1 year, so that some interannual variation may be averaged out, and some cases where a single year's estimate of soil respiration was compared to a single year's litterfall (predominantly the previous autumn's litterfall in temperate forests). Although a site may be near steady state in terms of decadal changes in soil and forest floor C stocks, there could be important variation in these pools on annual time scales due to interannual variation in herbivory, in climatic effects on foliage production, litterfall, and decomposition, and in allocation to seeds and other reproductive structures (Pregitzer and Burton, 1991). Some of the divergence from the regression line in Fig. 2 could be due to these variations that violate the near-steady-state assumption over the time scales common for short-term ecological studies.

Using data from our long-term study at the Harvard forest (Savage and Davidson, 2001), we compared annual litterfall and soil respiration for 4 years in each of five study plots (Fig. 5). Soil respiration varied among years, with the largest emissions recorded during wet summers of 1998 and 2000 and the lowest during the dry summer of 1999. Litterfall, in contrast, was relatively similar among the years of 1996–1999. We found no significant correlations between litterfall and soil respiration, either among years or among study plots within years. We conclude that the interannual differences in soil respiration were due more to climatic effects on decomposition and/or TBCA than to differences in the previous autumn's litterfall.

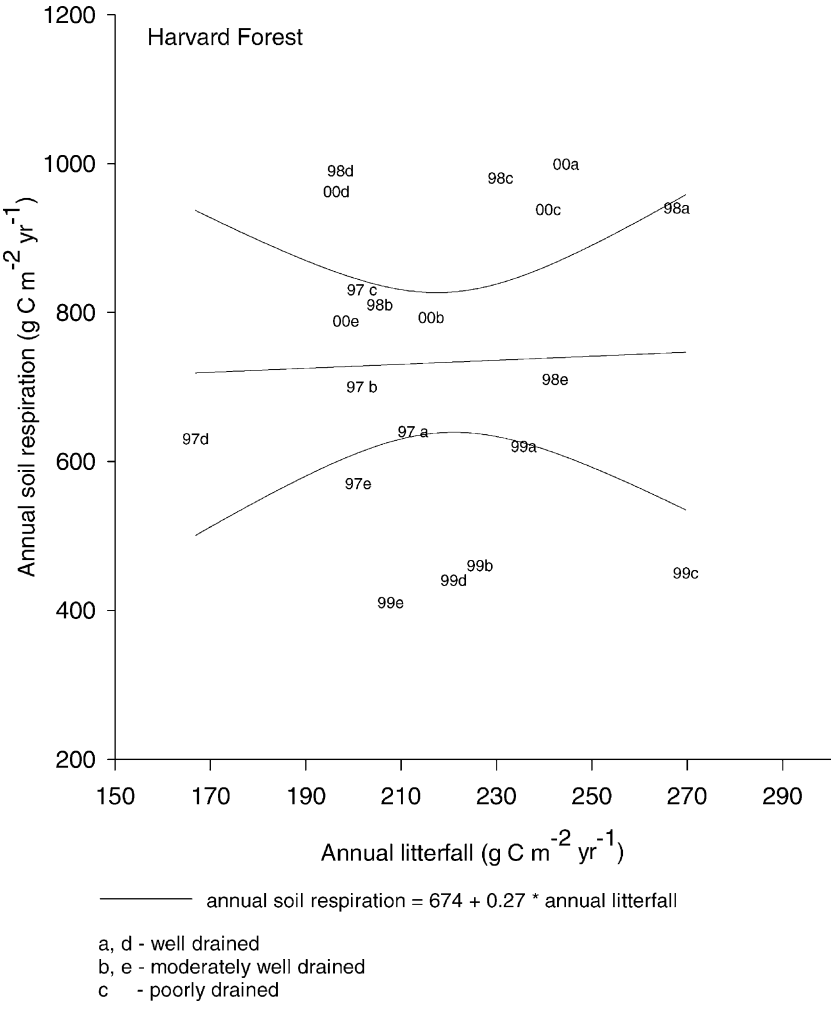

Fig. 5. Regression of annual soil respiration and annual aboveground litterfall-C for 4 years of observations (1997–2000) at five locations a–e (stratified by soil drainage class) in the Harvard forest, Massachusetts (Savage and Davidson, 2001). The annual soil respiration for each site and year is plotted against the previous year's litterfall-C for that site because most of the litterfall occurs in the autumn. The regression is not significant ($\alpha > 0.05$; $R^2 < 0.01$).

Although interannual variation in litterfall was not large at the Harvard forest, litterfall varied substantially between years at La Selva, Costa Rica. Only 1 of 2 years of available data was used for the La Selva site in the regression analysis in Fig. 2, because it was recognized that the litterfall during the second year was unusually large due to a severe El Nino event. Elevated litterfall in 1 year will presumably affect soil respiration in subsequent years, but observations over several years are needed to integrate these events into long-term averages. In the case of El Nino effects, a minimum of a 4–5-year period that matches the return interval of El Nino events may be needed to make the best comparisons of mean annual litterfall and soil respiration.

Comparisons of annual soil respiration to annual litterfall could reveal interannual variation of aboveground and belowground C allocation, but it would be difficult to distinguish between this interannual variation in inferred C allocation and short-term non-steady-state gain or loss in the forest floor C stock. The soil respiration-minus-litterfall approach

for estimating TBCA, which depends upon the near-steady-state assumption, is best applied to data averaged over several years, where the steady-state assumption is more likely to be nearly correct.

5. Conclusion

This analysis of forests from around the world, including new data from the Ameriflux network, has reconfirmed the general conclusion of Raich and Nadelhoffer (1989) that total belowground C allocation (TBCA) is usually at least two times the aboveground litterfall-C in mature forests. We found a non-zero *Y*-intercept to this relationship, indicating that TBCA may be more than two times litterfall-C where litterfall rates are relatively low. Regression lines for analyses of mature and young forests were not coincident, with a marginally significantly steeper slope for the young forests possibly indicating greater TBCA allocation relative to litterfall than observed in most mature forest. Not surprisingly, significant variation among sites and among years within sites was observed, indicating that estimates of annual TBCA from litterfall-C and soil respiration are probably improved by averaging over multiple years. The global relationship is generally robust and demonstrates that TBCA is the single largest flux of C in forest ecosystems aside from canopy assimilation.

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