A GLOBAL TREND IN BELOWGROUND CARBON ALLOCATION: COMMENT

Knute J. Nadelhoffer,1 James W. Raich,2 and J. D. Aber3

Gower et al. (1996) have questioned the validity of using a global-scale relationship between litterfall and belowground carbon (C) allocation (Raich and Nadelhoffer 1989) at stand and regional scales. We encourage attempts to understand better the controls on C allocation to roots in forests, including efforts to evaluate the potentials and limitations of C budgets for this purpose. However, the tests of our C-balance model that were presented by Gower et al. use inappropriate comparisons and the conclusions they drew are unwarranted. In addition, they misinterpret and misapply our C-budgeting models and their conceptual bases. Therefore, we clarify our approach to estimating belowground C allocation (Raich and Nadelhoffer 1989; Nadelhoffer and Raich 1992) and highlight problems with the tests of our models as conducted by Gower et al.

The issue in question is whether simplified soil C budgets can be used to estimate total root carbon allocation (TRCA, the annual rate at which assimilated C is allocated to producing and maintaining roots and mycorrhizae) in forest ecosystems. The conceptual model underlying the statistical model we used to predict TRCA at global scales (Raich and Nadelhoffer 1989) is based on the First Law of Thermodynamics (i.e., conservation of mass) and can be expressed as

\[
TRCA \approx \text{soil respiration} - \text{litterfall} + \text{export} + \Delta C_{\text{root}} - \Delta C_{\text{soil}} \tag{1}
\]

where units are grams of C per square meter per year and soil respiration is CO\textsubscript{2}-C released from the soil surface due to respiration by live roots and heterotrophs, litterfall is inputs to soil from aboveground production, export is C loss via erosion and leaching, \(\Delta C_{\text{root}}\) is the change in root C (fine + coarse), and \(\Delta C_{\text{soil}}\) is the change in soil C (forest floor plus mineral soil). The statistical model (same units) describes a simple linear regression that was derived from a collation of available data in which \((\text{export} + \Delta C_{\text{root}} - \Delta C_{\text{soil}})\) was assumed to be small relative to C fluxes in litterfall and soil respiration. The published statistical model is

\[
TRCA = 1.92 \times \text{litterfall} + 130. \tag{2}
\]

This relationship suggests that C allocation to roots (for tissue production plus respiration) in forests increases with litterfall at the global scale.

The statistical model (Eq. 2) is useful for estimating C allocation to roots only when certain conditions are met (see Raich and Nadelhoffer 1989). First, reliable measurements of annual litterfall and soil respiration rates are required. These are relatively easily made, but details of the methods used must be evaluated in order to assess the quality of model inputs. Second, the model is applicable only in relatively mature forests with “... soils that are near steady state with respect to total organic carbon storage” (Raich and Nadelhoffer 1989: 1347). In other words, the terms “export,” “\(\Delta C_{\text{root}}\)” and “\(\Delta C_{\text{soil}}\)” (Eq. 1) must be small relative to the other two terms in the conceptual model. Importantly, the model does not apply to young or to experimentally manipulated (e.g., fertilized, recently thinned) stands where C fluxes into and from soils can differ greatly and where changes in soil C pools can be large. We emphasize that soils should be near, but need not be at, steady state for application of the model. By stating otherwise, Gower et al. have misrepresented our model.

Criticism by Gower et al. of the use of C budgets is directed toward our published statistical relationship (Eq. 2) and focuses on three points: (1) the lack of a positive correlation between measured and predicted belowground C allocation; (2) the lack of a positive relationship between estimated fine-root production and predicted belowground C allocation; and (3) the potential misuse of our approach even if it is valid. Points (1) and (2) are legitimate attempts to invalidate the approach. Point (3) is misdirected in that the validity of the approach is questioned based on its potential for misuse. We respond below to each point.

Point 1.—The comparison between measured and predicted TRCA (Gower et al. 1996: Fig. 1) is not an appropriate test of our statistical model (Eq. 2) or of the overall C-budgeting approach because it is based on inappropriate data. Of the stands used in their com-
parison, only 3 of 17 were >30 yr old and were neither fertilized, irrigated, or thinned (Gower et al. 1996: Table 1). Assuming that soil C content is near steady state in such stands is not realistic. Furthermore, methods used to estimate litterfall and soil respiration in 8 of their 17 stands are unpublished and therefore unverifiable. Data from four additional stands were not published as of November 1997 and data from two others were published in a non-refereed and unavailable symposium proceedings. Thus, methods for estimating litterfall and soil respiration were not specified for 16 of the 17 stands used in their comparison. Given the uncertainties and potential problems associated with methods for estimating soil C fluxes, methods and the predictor variable of TRCA (i.e., litterfall) at a global scale, “[for all data sets combined . . . there was no correlation between [fine-root production] estimates and litterfall]” (Nadelhoff and Raich 1992: 1142). The “test” of our statistical model as applied to temperate forests by Gower et al., therefore, was essentially the same relationship as we reported at a global scale (Nadelhoff and Raich 1992: Fig. 1). In fact, values from 23 of the 34 temperate-forest stands used in Gower et al. (1996) were used in our previous analysis (Nadelhoff and Raich 1992, with data from McGinty 1976, Harris et al. 1977, Grier et al. 1981, McClaugherty et al. 1982, Aber et al. 1985, Gholz et al. 1985, 1986, Nadelhoff et al. 1985, Ellenberg et al. 1986, Joslin and Henderson 1987, Monk and Day 1988, Symbula and Day 1988, van Praag et al. 1988). The difference was that Gower et al. transformed litterfall (their independent variable) into predicted TRCA (their independent variable) prior to conducting their analysis. Furthermore, although Gower et al. (1996:1753) state that “There is . . . disagreement . . . as to the accuracy of various methods used to estimate belowground carbon dynamics,” they focus primarily on uncertainties associated with TRCA estimates and do not incorporate uncertainties in FRP estimates into their discussion. Instead, they use the lack of a significant correlation as an opportunity to speculate about possible factors that might cause patterns of aboveground and belowground C allocation by trees to vary from stand to stand. The likely possibility that methodological problems might compromise existing FRP estimates was omitted from their abstract in favor of this speculation.

Point 3.—Gower et al. (1996: 1750) express a well-founded concern that “. . . it may not be wise to use the [Raich-Nadelhoff] model to estimate total root C allocation for specific stands where conditions may deviate significantly from the averages reflected in the data on which the model was based.” However, the possibility that an average or model may be misused does not serve to invalidate that technique or model. We agree that our model should not be used in situations where its underlying assumptions cannot be met. Unfortunately, these authors ignored their own dictum by applying our statistical relationship to a data set in which most of the stands were either grading (<30 yr old) or were recently thinned, irrigated, or fertilized. Soil C stocks in these stands were unlikely to be near steady state as the experimental manipulations likely altered primary production (C inputs to soils) and microbial activity (a major component of soil respiration). Therefore, a fundamental assumption of the model was violated in an attempt to test it. As such, their exercise fails to support the conclusion that our statistical model does not apply at less-than-global scales.

We agree with Gower et al. that site-specific measurements of TRCA (referred to as “TRCA-M” by these authors and based on Eq. 1) are superior to model-based predictions (“TRCA-RN,” from Eq. 2). We did not suggest otherwise in either of our papers (Raich and Nadelhoff 1989, Nadelhoff and Raich 1992). Nor did we suggest, as implied by these authors, that litterfall alone may be used to define a soil C budget. We do maintain that until our statistical model is objectively invalidated, its use in generalized forest ecosystem models such as those of Aber and Federer (1992) and Ryan and Waring (1992) is justified.

Can carbon budgets be used to constrain fine root production estimates?

To illustrate how C budgets can be used to assess FRP estimates, we synthesize published values of C fluxes in a ~180-yr-old Abies amabilis stand described by Vogt et al. (1980, 1982) and Grier et al. (1981). At this site FRP was 554 g m⁻² yr⁻¹ (Gower et al. 1996, from Grier et al. [1981] and derived from sequential coring), litterfall was 106 g C m⁻² yr⁻¹ (from Grier et al. 1981), and soil respiration was 620 g C m⁻² yr⁻¹.
(estimated from Vogt et al. 1980: Fig. 5). Therefore, the sum of C inputs from litterfall and estimated FRP (660 g·m\(^{-2}·yr\(^{-1}\)) exceeds measured soil respiration. This budget does not include the contribution to soil respiration from live-root respiration, which is at least equal to the C allocation to fine-root biomass (Mooney 1972, Penning de Vries 1975). Thus, a simplified soil C budget applied to this stand using on-site measurements of litterfall and soil respiration suggests that either the published estimate of FRP for this stand is unrealistically high or soil C accumulation was 600 g·m\(^{-2}·yr\(^{-1}\)), 5 times the measured C inputs via litterfall. We think the latter is unlikely and conclude that FRP at this site was greatly overestimated. Rather, we use this extreme value (which, together with data from a younger A. amabilis stand located nearby the 180-yr-old stand) contribute strongly to the negative correlation between FRP and model-based predictions of TRCA reported in Gower et al. (1996) to illustrate problems inherent in estimating FRP using root-biomass measurements.

Summary and conclusions

Gower et al. (1996) provided no new insights into either the validity or the utility of the global-scale analysis of Raich and Nadelhoffer (1989). Gower et al. avoided addressing the use of soil C budgets to constrain estimates of fine-root production as proposed by Nadelhoffer and Raich (1992), and they presented no data showing that soil C budgets, if used appropriately, are unsuitable for use at stand, biome, or regional scales. Until better data become available, we must take advantage of existing information on forest C fluxes and recognize the fact that everything goes somewhere. Fluxes of C to roots that exceed annual C inputs to soils from aboveground sources by factors of ≥2 must be accounted for as increases in soil C or as measured losses (via respiration or other processes). We contend that statements such as “76% of annual total net primary production by forests [may be] allocated to fine roots” (Gower et al. 1996:1750) are insupportable unless the fate of such large allocations to roots can be accounted for in other ecosystem pools or fluxes.

The soil C-budgeting approach (Eq. 1) is one means of estimating total annual C fluxes to roots. It is based on the principle of conservation of mass and can be used to investigate belowground C fluxes in forests at local, regional, and global scales. Total C allocation to roots is estimated as the difference between C inputs via soil respiration in stands where C pools can be assumed as near steady state. When soil C is not near steady state, for example in aggrading or in recently disturbed forests, then additional terms (i.e., export, ΔC\(_{\text{root}}\), and ΔC\(_{\text{soil}}\) in Eq. 1) are required to reliably estimate belowground allocation using C budgets.

We concur with Gower and coauthors that the global-scale statistical relationship we derived using forest C budgets (Raich and Nadelhoffer 1989) should be evaluated at smaller scales. In our opinion, however, conclusions derived from our global-scale model, namely (a) that TRCA increases with aboveground net primary production (ANPP) and (b) that TRCA : ANPP decreases along global resource-availability gradients, form the basis of realistic working hypotheses about controls on root : shoot C allocation in mature, closed-canopy forests. Fair and objective evaluations of these conclusions using data from different sites than those used to develop the original model are clearly needed, as are continued efforts to identify how C-allocation patterns in forests vary in relation to stand age, species composition, and management practices.

Acknowledgments

This work was supported by the Harvard Forest Long-Term Ecological Research project (NSF-DEB-9411975), the Iowa Center for Global and Regional Environmental Research, and the USDA-NRI CG Program grant number 95-37102-2213. Support by the Norwegian Institute for Water Research and the U.S. Fulbright Foundation is also gratefully acknowledged.

Literature cited


THE RELATIONSHIP BETWEEN LOCAL AND REGIONAL DIVERSITY: COMMENT

Mark Westoby

Caley and Schluter (1997) compiled data on local vs. regional species richness, and arranged it following a graphical method proposed by Cornell (1985, 1993, Cornell and Lawton 1992). They concluded that local assemblages were not saturated with species. This comment argues that the procedure and reasoning they used has flaws, and should not be generally adopted. The comment is agnostic about the substantive issue of saturation, and addresses only the issue of much weight should be given to the evidence presented by Caley and Schluter.

Inappropriate scale for "local" assemblages

Interest in testing whether local assemblages are saturated with species arises out of literature on species interactions within assemblages. The underlying idea is that a local assemblage is one where the component species are interspersed and interact with each other, affecting local persistence or extinction. The processes that might hypothetically cause saturation are interactions between species populations.

The smallest areas used by Caley and Schluter to represent local species richness were cells 50 × 50 km. (They also investigated cells 10 times that area, and regional species richness was counted in cells 500 × 500 km.) Of course it could be argued that the definition of “local” is just a matter of semantics. But in the context of discussions about species saturation, the point is that few would expect convergence of species richness due to within-community interactions to operate at a 50 × 50 km scale. To take land plants as an example, only small subsets of the species list in 50 × 50 km would occur as interspersed populations. Most species would be separated onto different landscape elements within the 50 × 50 km cell.

Manuscript received 1 April 1997; accepted 24 April 1997; final version received 4 February 1998.

¹ School of Biological Sciences, Macquarie University, New South Wales 2109, Australia.