Fine Root Production Estimates and Belowground Carbon Allocation in Forest Ecosystems

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Knute J. Nadelhoffer
University of Michigan
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Iowa State University
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FINE ROOT PRODUCTION ESTIMATES AND BELOWGROUND CARBON ALLOCATION IN FOREST ECOSYSTEMS[1]

KNUTE J. NADELHOFFER AND JAMES W. RAICH[2]
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA

Abstract. We compared published estimates of net fine root production (FRP) in forest sites to litterfall and aboveground net primary production (ANPP) to test whether annual rates of fine root and aboveground production vary together at global scales. We also compared FRP estimates to theoretical upper limits as defined by our previously published relationship between total root allocation (TRA, carbon allocated to FRP plus live-root respiration) and litterfall. Estimates of the carbon content of FRP in the total data set ranged from 25 to 820 $g \cdot m^{-2} \cdot yr^{-1}$ and were not correlated with annual litterfall or ANPP. Different methods used for estimating fine root production, however, showed contrasting results. Estimates derived using either sums of seasonal changes in fine root biomass ("Sequential Core" method) or differences between annual maximum and minimum fine root biomass ("Maximum − Minimum" method) were not correlated with either litterfall or ANPP. Sequential Core estimates were often high relative to predicted TRA values, whereas Maximum − Minimum estimates were generally <50% of TRA. The small number of FRP estimates derived from root growth into root-free cores ("Ingrowth Core" method) were not correlated with measures of aboveground production but were all well below predicted TRA values. In contrast to results of other methods, FRP estimates derived using ecosystem N budgets ("N Budget" method) were positively correlated with both litterfall and ANPP. Comparing FRP estimates based on N budgets with previous results of forest soil C budgets suggested that annual fine root production increases with aboveground production and that ≈⅓ of TRA is used for production of fine roots.

Key words: belowground production; carbon budgets; fine roots; forests; net primary production; nitrogen budgets; root production.

INTRODUCTION

Measuring fine root production in terrestrial ecosystems is problematic. It is therefore difficult to generalize about relationships between belowground and aboveground production or about controls on fine root production. Nevertheless, fine root production likely represents a large proportion of total annual net primary production in most ecosystems. For example, some studies suggest that fine root production in forest ecosystems might account for up to 75% of total net primary production (Ågren et al. 1980, Grier et al. 1981, Vogt et al. 1982, 1986b, Fogel 1983). Such conclusions must be considered tentative, however, because all methods used for measuring fine root production are indirect and are subject to uncertainties and possible biases (Singh et al. 1984, Lauenroth et al. 1986, Sala et al. 1988). Therefore, our ability to test whether any overall relationships between below- and aboveground production exist in forests or other ecosystems has been compromised.

Our previous analysis of forest soil carbon (C) budgets showed that total annual C allocation to roots (i.e., the sum of net fine root production and live-root res-

piration) increases with litterfall on a global scale (Raich and Nadelhoffer 1989). If annual C allocation below- and aboveground is controlled by the same factors as suggested by our global-scale analysis, then fine root production, a large component of belowground C allocation, could also increase along large-scale gradients of aboveground production.

In this paper we use published data to test the null hypothesis that annual rates of net fine root and aboveground production in forest ecosystems are not related. Rejection of the null hypothesis would suggest that similar factors control net production both below- and aboveground. We specifically consider how different methods for estimating annual fine root production can affect conclusions about whether belowground and aboveground production are related.

METHODS

We compiled 59 published estimates of annual net fine root production (FRP) from 43 forest sites worldwide at which aboveground litter production, aboveground net primary production, or both were also measured (Table 1). We compared estimates of net FRP to litterfall because litterfall is measured with relatively simple and accurate methods and because litterfall C was a critical factor in estimating total C allocation to fine roots in our previous analysis of forest soil C budgets (Raich and Nadelhoffer 1989). We also compared

TABLE 1. Data used in analyses of fine root studies. ANPP refers to aboveground net primary production and FRP refers to net fine root production.

Site, location	Litter-fall (g·m⁻²·yr⁻¹)	ANPP (g·m⁻²·yr⁻¹)	FRP (g·m⁻²·yr⁻¹)	Meth-od*	Reference
120-yr-old Scots pine, Sweden	135	285			Bringmark 1977
120-yr-old Scots pine, Sweden			217	A	Persson 1983
120-yr-old Scots pine, Sweden			226	C	Persson 1983
Terra firme forest, Venezuela	990	1590			Medina and Cuevas 1989
Terra firme forest, Venezuela			1540	A	Vitousek and Sanford 1986
Terra firme forest, Venezuela			201	C	Jordan and Escalante 1980
Terra firme forest, Venezuela			1117	C	Cuevas and Medina 1988
Tall caatinga, Venezuela	710	1150			Medina and Cuevas 1989
Tall caatinga, Venezuela			120	C	Cuevas and Medina 1988
Black oak, southern Wisconsin, USA	590†	1103	591	D	Nadelhoffer et al. 1985
Black oak, southern Wisconsin, USA			174	B	Aber et al. 1985
Red oak, southern Wisconsin, USA	596†	1371	524	D	Nadelhoffer et al. 1985
Red oak, southern Wisconsin, USA			52	B	Aber et al. 1985
White oak, southern Wisconsin, USA	516†	1085	413	D	Nadelhoffer et al. 1985
White oak, southern Wisconsin, USA			115	B	Aber et al. 1985
Sugar maple, southern Wisconsin, USA	410†	932	402	D	Nadelhoffer et al. 1985
Sugar maple, southern Wisconsin, USA			110	B	Aber et al. 1985
Birch, southern Wisconsin, USA	406†	680	324	D	Nadelhoffer et al. 1985
White pine, southern Wisconsin, USA	410†	837	257	D	Nadelhoffer et al. 1985
White pine, southern Wisconsin, USA			97	B	Aber et al. 1985
Mixed pine, southern Wisconsin, USA	446†	850	262	D	Nadelhoffer et al 1985
Spruce, southern Wisconsin, USA	383†	748	160	D	Nadelhoffer et al. 1985
Red pine, southern Wisconsin, USA	360†	653	198	D	Nadelhoffer et al. 1985
Red pine, southern Wisconsin, USA			69	B	Aber et al. 1985
Red pine, central Wisconsin, USA	243†				J. Pastor, personal communication
Red pine, central Wisconsin, USA		410	253	B	Aber et al. 1985
Red pine, central Wisconsin, USA			120	D	Aber et al. 1985
White pine, central Wisconsin, USA	310	640			McClaugherty et al. 1985
White pine, central Wisconsin, USA			162	B	Aber et al. 1985
White pine, central Wisconsin, USA			140	D	Aber et al. 1985
White oak, central Wisconsin, USA	300	840			McClaugherty et al. 1985
White oak, central Wisconsin, USA			340	D	Aber et al. 1985
White oak, central Wisconsin, USA			305	B	Aber et al. 1985
Red oak, central Wisconsin, USA	357†				J. Pastor, personal communication
Red oak, central Wisconsin, USA		810	235	B	Aber et al. 1985
Red oak, central Wisconsin, USA			250	D	Aber et al. 1985
Sugar maple, central Wisconsin, USA	380				McClaugherty et al. 1985
Sugar maple, central Wisconsin, USA		950	106	B	Aber et al. 1985
Sugar maple, central Wisconsin, USA			650	D	Aber et al. 1985
Red pine, Massachusetts, USA	726				Vitousek et al. 1982
Red pine, Massachusetts, USA		980	420	D	Aber et al. 1985
Red pine, Massachusetts, USA			1090	A	McClaugherty et al. 1982
Red pine, Massachusetts, USA			410	B	McClaugherty et al. 1982
Mixed hardwoods, Massachusetts, USA	489				Vitousek et al. 1982
Mixed hardwoods, Massachusetts, USA		930	400	D	Aber et al. 1985
Mixed hardwoods, Massachusetts, USA			1140	A	McClaugherty et al. 1982
Mixed hardwoods, Massachusetts, USA			540	B	McClaugherty et al. 1982
180-yr-old fir, Washington, USA	218	455	1708	A	Vogt et al. 1982
Liriodendron, Tennessee, USA	433	865			Stand No. 23, Cole and Rapp 1981
Liriodendron, Tennessee, USA			900	A	Harris et al. 1977
Liriodendron, Tennessee, USA			580‡	B	Harris et al. 1977
Pinus elliottii, Florida, USA	499				Gholz et al. 1985b
Pinus elliottii, Florida, USA		1346			Gholz and Fisher 1982
Pinus elliottii, Florida, USA			542	E	Gholz et al. 1985a
120-yr-old Fagus, Belgium	486†		439	A	van Praag et al. 1988
35-yr-old Picea, Belgium	343†		701	A	van Praag et al. 1988

TABLE 1. Continued.

Site, location	Litter-fall (g·m⁻²·yr⁻¹)	ANPP (g·m⁻²·yr⁻¹)	FRP (g·m⁻²·yr⁻¹)	Method*	Reference
Pseudotsuga, dry site, Oregon, USA	286†				Santantonio 1982
Pseudotsuga, dry site, Oregon, USA			650	A	Santantonio and Hermann 1985
Pseudotsuga, moderate site, Oregon, USA	236†				Santantonio 1982
Pseudotsuga, moderate site, Oregon, USA			630	A	Santantonio and Hermann 1985
Pseudotsuga, wet site, Oregon, USA	307†				Santantonio 1982
Pseudotsuga, wet site, Oregon, USA			480	A	Santantonio and Hermann 1985
Deciduous forest, fenced, India	569	950			Singh and Misra 1979, as cited by Cannell 1982
Deciduous forest, fenced, India			279	B	Singh and Singh 1981
Deciduous forest, unfenced, India	505	839			Singh and Misra 1979, as cited by Cannell 1982
Deciduous forest, unfenced, India			241	B	Singh and Singh 1981
Quercus spp., Missouri, USA	518		220	A	Joslin and Henderson 1987
Quercus spp., Missouri, USA		598			Rochow 1975
Pseudotsuga, low site, Washington, USA	286†	730	620	B	Keyes and Grier 1981
Pseudotsuga, low site, Washington, USA			700	E	Keyes and Grier 1981
Pseudotsuga, high site, Washington, USA	457†	1370	160	B	Keyes and Grier 1981
Pseudotsuga, high site, Washington, USA			250	E	Keyes and Grier 1981
Pseudotsuga, Oregon, USA	386	1180	1668§	A	Fogel and Hunt 1983
Pinus contorta, xeric 1, Brit. Col.	170	350	390	A	Comeau and Kimmins 1989
Pinus contorta, xeric 2, Brit. Col.	170	330	590	A	Comeau and Kimmins 1989
Pinus contorta, mesic 1, Brit. Col.	270	640	470	A	Comeau and Kimmins 1989
Pinus contorta, mesic 2, Brit. Col.	400	740	370	A	Comeau and Kimmins 1989
Fagus, Germany	436	1030	150	A	Ellenberg et al. 1986
Nyssa–Acer swamp, Virginia, USA	658		597‖	C	Symbula and Day 1988
Nyssa–Acer swamp, Virginia, USA			645‖	A	Symbula and Day 1988
Nyssa–Acer swamp, Virginia, USA		1050			Megonigal and Day 1988
Quercus–Carya, North Carolina, USA	440	840			Monk and Day 1988
Quercus–Carya, North Carolina, USA			600#	C	McGinty 1976, Monk and Day 1988

* Methods: A = Sequential Core; B = Maximum − Minimum; C = Ingrowth Core; D = Nitrogen Budget; E = various other.

† Litterfall estimated from leaf litterfall or foliage production assuming leaf litterfall (or foliate production) equals 70% of total fine litterfall, following Meentemeyer et al. (1982).

‡ Not used as a root production estimate by the cited author(s); value determined from data or figures in cited papers.

§ Described as throughput by authors. Cited value includes fine roots and mycorrhizae, and is considered to be a conservative estimate (Fogel 1983).

‖ Total for 11 mo only.

No diameter size classes reported: all roots were harvested.

estimates of annual fine root production with measures of total aboveground production to examine the nature of overall relationships between below- and aboveground production.

Fine roots are generally defined as nonwoody, small-diameter roots and mycorrhizae. Upper values for fine root diameters vary among published studies and generally range from <1 to ≤5 mm. Definitions of fine roots vary among studies because fine root morphology and size vary among species and even within species across sites (Fitter 1985). Because criteria used to identify fine roots are not uniform, we considered fine roots to be as defined in the cited studies. We classified studies according to one of four general methods in order to determine whether different methods lead to similar or different conclusions.

Two common methods, the "Sequential Core" and the "Maximum − Minimum" techniques, use changes in fine root biomass in volumetric soil samples to estimate fine root production. Biomass estimates are generally obtained by separating live fine roots from soils in spatially replicated soil cores. Both methods require repeated estimates of fine root biomass over the course of at least one year or growing season.

Results based on the Sequential Core method refer to production estimates calculated as differences in means of fine root biomass between sampling periods summed across growing seasons (Fogel 1983, Fairley

and Alexander 1985). The Sequential Core studies we analyzed differed in timing and intensity of sampling and in algorithms used to estimate annual fine root production. For example, some estimates were derived from sums of increases in fine root biomass between sampling times while others were derived from sums of decreases. Some investigators used only significant differences, and others used all observed differences in sample means. Occasionally, changes in fine root necromass were used to estimate production or to correct for simultaneous growth and death during a sample interval. Such differences and their influences on FRP estimates are more fully discussed by Fogel (1983) and Fairley and Alexander (1985). Regardless of these methodological variations, we classified studies that used summed differences in means of fine root biomass sampled sequentially over the course of either growing seasons or calendar years as using the Sequential Core technique.

The Maximum − Minimum method is simpler than the Sequential Core method in that it uses only the difference between annual minimum and maximum fine root biomass to estimate FRP (Edwards and Harris 1977, McClaugherty et al. 1982, Aber et al. 1985). We classified results from studies that used differences between peak and minimum fine root biomass to estimate production as being based on the Maximum − Minimum method, even if fine root biomass was estimated more than twice annually.

A third technique for estimating fine root production is the "Ingrowth Core" method. This method uses measurements of fine root growth into a root-free medium placed in the soil profile to estimate production (Flower-Ellis and Persson 1980, Jordan and Escalante 1980, Persson 1983). Fine root growth into sieved soil cores, trenched plots, leaf litter samples, and artificial materials (e.g., vermiculite) have been used over a range of time periods to estimate production. Regardless of the specific material, plot size, or time period used, we classified any FRP estimate derived from root growth into root-free material as being based on the Ingrowth Core technique.

The final method considered herein is the "Nitrogen (N) Budget" method. This method requires annual measures of net N mineralization in soil and net N flux into aboveground tissues. Annual N allocation to fine roots is calculated as the difference between net N mineralization and net N fluxes into aboveground tissues. Estimated FRP is then calculated as the product of annual N allocation to fine roots and the C:N ratio in fine roots (Aber et al. 1985, Nadelhoffer et al. 1985).

In contrast to the variety of methods used to estimate FRP, most estimates of aboveground litter production we used were derived from litterfall into traps on the forest floor. Some litter production estimates in conifer forests, however, were calculated as the product of foliage biomass and foliar turnover rates. Litterfall estimates typically emphasize overstory and shrub lit-

terfall whereas most estimates of forest root production include contributions from overstory trees, shrubs, and understory vegetation.

We converted all organic matter (OM) fluxes to carbon units using a C:OM of 0.48. This allowed for direct comparison of fine root production measurements and total root C allocation on an annual basis. Total root C allocation (TRA), or the sum of FRP and live-root respiration, was estimated using litterfall C (LFC) as a predictor: TRA = 130 + 1.92(LFC) (from Raich and Nadelhoffer 1989). Data used previously to identify the relationship between total root C allocation and litterfall were from a different set of litterfall and soil respiration values than are used here to compare net FRP and litterfall.

Relationships between net FRP and aboveground production were analyzed using least-squares linear regression (SAS 1987: release 6.03), first with litterfall and second with net aboveground production as independent variables. The null hypothesis was rejected if the slope of the relationship between FRP and litterfall or between FRP and aboveground production differed significantly ($P < .05$) from zero.

RESULTS

Along a gradient of litterfall C ranging from 65 to 475 $g \cdot m^{-2} \cdot yr^{-1}$, estimates of the carbon content of FRP ranged from 25 to 820 $g \cdot m^{-2} \cdot yr^{-1}$. For all data sets combined (Table 1), there was no correlation between FRP estimates and litterfall ($r^2 = 0.04$, $n = 59$). Results differed, however, according to methods used to estimate FRP. Correlations between FRP estimates and litterfall were not significant for studies that used either Sequential Core, Maximum − Minimum, or Ingrowth Core techniques (Fig. 1A–C). In contrast, estimates of FRP made using the N Budget technique were positively correlated with litterfall (Fig. 1D).

Estimated FRP values also differed among methods with respect to approximate upper limits on total carbon allocation to roots as previously calculated using forest soil C budgets (cf. Raich and Nadelhoffer 1989). Estimates of carbon allocated to FRP derived using the Sequential Core method were often about equal to and sometimes greater than predicted total root allocation of carbon (Fig. 1A). In contrast, most estimates derived using the Maximum − Minimum, Ingrowth Core, and N Budget methods were less than half of predicted total root allocation (Fig. 1B–D).

Carbon allocation to aboveground net primary production (ANPP) in these forests ranged from 137 to 763 $g \cdot m^{-2} \cdot yr^{-1}$. As with FRP and litterfall, there were no significant correlations between FRP estimates and ANPP for results of all methods combined ($r^2 = 0.05$, $n = 54$), or for results of Sequential Core ($r^2 = 0.23$, $n = 14$), Maximum − Minimum ($r^2 = 0.05$, $n = 18$), or Ingrowth Core ($r^2 = 0.13$, $n = 6$) methods. For results derived from the N Budget method, however, the cor-
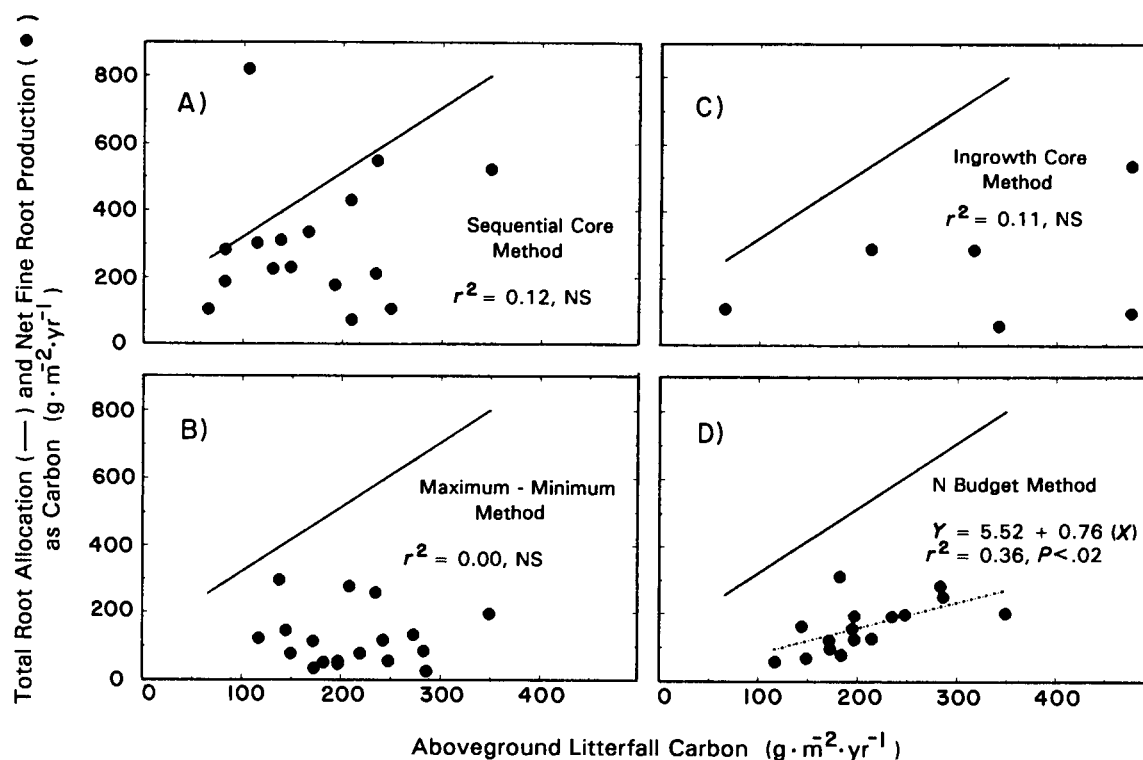
FIG. 1. Fine root production estimates vs. litterfall in forest ecosystems. Values are from published studies (Table 1) in which fine root production was estimated using four different techniques (see *Methods*). Solid lines show total root allocation [TRA (= root respiration + root production)] of C as predicted from litterfall C [$Y = 130 + 1.92(X)$, from Raich and Nadelhoffer 1989].

relation between FRP and ANPP was highly significant and was described by the least squares regression: FRP $= -70 + 0.56(ANPP)$ ($r^2 = 0.63$, $P < .0002$, $n = 16$).

DISCUSSION

Conclusions about the magnitude of annual fine root production and about the nature of any relationship between annual rates of fine root and aboveground production in forests depend on methods used to estimate fine root production. Estimates of FRP derived using differences in fine root biomass (Fig. 1A, B) and estimates derived using fine root ingrowth into cores (Fig. 1C) do not allow for rejecting the null hypothesis (H_0: rates of fine root and aboveground litter production are unrelated). In other words, results derived from these methods show no evidence of overall trends of either increase or decrease in annual fine root production along gradients of aboveground production. In contrast, the significant positive correlations between FRP estimates derived using N budgets and both litter production (Fig. 1D) and ANPP result in rejection of H_0 and suggest that production of fine roots and production of aboveground tissues increase together.

It is useful to compare the alternative relationships between FRP and aboveground production suggested by different methods with soil respiration (SR), a pro-

cess that is linked to both fine root and aboveground production. SR is the release of CO_2 from soil due to respiration by decomposers (which oxidize organic carbon derived largely from fine root detritus and aboveground litter) and live roots. We recently reported a correlation between SR and litterfall in a global-scale comparison of forest soil C budgets (Raich and Nadelhoffer 1989). We also showed that total root allocation (TRA, C allocated to FRP plus live root respiration) can be estimated by subtracting C released due to decomposition of aboveground litter from total SR and that TRA increased by ≈ 2 C units for every unit increase in litterfall at a global scale. This suggested that respiration of live roots, production of fine roots, or both processes together, increase with ANPP at large geographic scales.

Because TRA is the sum of C allocated to production plus respiration of fine roots, the observed relationship between TRA and litterfall defines the approximate upper limits of FRP along gradients of litter production for sites at which annual changes in soil C stocks are low relative to C inputs. Because more C is released from live roots to support construction and maintenance respiration than is allocated to structural components of tissues (Mooney 1972, Penning de Vries 1975, Chapin 1989), C allocation to FRP should be no more than half of TRA at a given site. In other words,

more C is used to support fine root respiration than is allocated to the production of fine root tissue.

The accuracy and reliability of methods used for estimating FRP must also be considered to determine which conclusion about the relationship between belowground and aboveground production is more realistic. All four methods used to estimate FRP at the scale of whole ecosystems are indirect and subject to errors and unintended biases. Therefore, we also consider possible sources of errors for individual methods and how such errors can affect conclusions about patterns of FRP.

The observation that a large proportion of FRP estimates derived using the Sequential Core method is high relative to the approximate upper limit imposed by the TRA function (Fig. 1A) is consistent with models showing that this method can yield large overestimates, especially when fine root biomass is large or spatially variable (Singh et al. 1984, Kurz and Kimmins 1987). These models showed that FRP estimates based on sequential biomass sampling are highly sensitive to sampling error. For example, simulated sampling from artificial but realistic data on fine root distributions by Singh et al. (1984) showed that sums of changes in biomass samples can be either lower or higher than true production. Increased frequency of sampling, however, does not necessarily increase the accuracy of FRP estimates. It can lead to large overestimates if changes in fine root biomass in samples do not reflect actual changes in the field (Sala et al. 1988). On the other hand, summing changes in fine root biomass can underestimate production if growth and mortality occur simultaneously (Kurz and Kimmins 1987) or if the timing of field sampling does not coincide well with actual periods of maximum and minimum fine root biomass (Vogt et al. 1986a). Much of the scatter in fine root production estimates within the set of Sequential Core results could be due to variations in the direction and magnitude of such biases among studies.

Estimates derived from the Maximum − Minimum method are generally well below the upper limits to FRP as derived from our previous TRA calculation (Fig. 1B). When sampling errors can be minimized, this method can be used to define a lower limit to FRP at a site. This method underestimates FRP, however, at sites where fine root biomass is not seasonally variable, where roots are short lived or where periods of production and mortality overlap (Aber et al. 1985, Kurz and Kimmins 1987). This method is best suited for use at sites where periods of maximum and minimum fine root biomass can be estimated with reasonable precision and where there is little overlap in fine root production and decomposition (McClaugherty et al. 1982, Aber et al. 1985).

Existing FRP estimates derived using Ingrowth Core methods all fall within the limits imposed by our global-scale analysis (Fig. 1C). However, the specific techniques utilized differed considerably among the studies cited (Table 1), and too few results of these techniques have been published to determine whether any relationship between FRP and aboveground production might exist. Therefore, conclusions based on this small set of studies should be viewed even more tentatively than results of other methods. The method does suffer some potential problems. Severing of live roots during placement of cores in soil profiles could affect ingrowth rates as could the nutrient status and structure of the medium into which root growth is measured. Nevertheless, more estimates using this method could be useful as it has yielded some interesting results (e.g., Ahlström et al. 1988).

All FRP estimates based on the N Budget method are below the theoretical limit imposed by the regression between TRA and litterfall (Fig. 1D). Also, results of N Budget studies show the same overall trend as did our previous global analysis (Raich and Nadelhoffer 1989): increasing annual allocation of C to fine root production along gradients of aboveground production. Realistic estimates of FRP based on N budgets require that in situ measures of net N mineralization in forest soils (Nadelhoffer et al. 1983, 1985, Pastor et al. 1984) yield realistic estimates of annual N uptake by vegetation and that measures of N uptake allocated to aboveground production are relatively accurate. Analyses of changes in mineral N pools in soils together with results of approximately monthly N mineralization measures suggest that in situ soil incubations can provide reasonable estimates of N uptake by vegetation in temperate and subalpine forest ecosystems (Nadelhoffer et al. 1984, Raison et al. 1987). The reliability of in situ incubations in other ecosystem types, however, remains untested. Nitrogen Budget estimates also assume that annual N loss from soil is low and that N retranslocation from senescing roots is unimportant. If substantial withdrawal of structural N from roots occurs prior to senescence, then the N Budget method would underestimate annual fine root production. Although retranslocation from senescing fine roots is possible (Goldfarb et al. 1990), we know of no published studies indicating this process is quantitatively important in fine roots.

Studies that used more than one method to estimate FRP present some useful insights. In three forests where Sequential Core and Maximum − Minimum methods were both used, estimates based on Sequential Cores were about double Maximum − Minimum estimates (Table 1; Harris et al. 1977, McClaugherty et al. 1982). The estimates derived by McClaugherty et al. (1982) using the Maximum − Minimum method for a red pine and a mixed-deciduous forest closely matched their estimates of N available to support annual fine root production. Also, Aber et al. (1985) reported good agreement between Maximum − Minimum and N Budget estimates for sites where fine root biomass showed strong seasonality but lower Maximum − Min-

imum estimates at sites where fine root biomass showed little or no seasonality. FRP estimates based on Ingrowth and Sequential Core methods matched well for some sites such as a mature scots pine plantation (Persson 1983), a *Nyssa–Acer* dominated swamp (Symbula and Day 1988), and a terra firme forest (Vitousek and Sanford 1986 vs. Cuevas and Medina 1988). Two FRP estimates (Jordan and Escalante 1980, Cuevas and Medina 1988) derived using the Ingrowth Core method at a terra firme site showed more than a five-fold difference (Table 1). This difference could reflect spatial or year-to-year variability in fine root production at this site. It might result partially from differences in applying the Ingrowth Core technique.

We recommend that annual FRP estimates derived by any method be compared with upper limits imposed by TRA. We emphasize, however, that our previously identified relationship (Raich and Nadelhoffer 1989) is approximate and ignores seasonal and yearly variations within sites. As such, our global analysis may have masked intersite differences in C allocation. Therefore, we suggest that future estimates of FRP be compared with TRA estimates derived from on-site measurements of litterfall and soil respiration.

Independent analyses of forest ecosystem element budgets suggest that fine root production plus respiration (C budgets) and that fine root production alone (N budgets) increase along large-scale gradients of aboveground production and that C allocation to fine root production could be ≈⅓ of total annual C allocation to roots (Fig. 2). If annual rates of fine root and aboveground production do increase together, then fine root turnover (production or mortality divided by biomass) would need to increase along production and resource gradients to allow for decreases in fine root biomass that have been commonly observed along these gradients (e.g., Grier et al. 1981, Nadelhoffer et al. 1985).

CONCLUSIONS

The reasons for the large variations in FRP reported for different forests and the lack of any relationship between FRP and aboveground production in the overall data accumulated to date are unclear. Either annual production of fine roots and aboveground biomass are not linked or errors in estimating fine root production are great enough to obscure evidence of an overall relationship. Important questions must be answered before we can reliably estimate annual fine root production at ecosystem scales using existing methods. How are N availability and N uptake by vegetation best measured? Do roots translocate N or other nutrients out of tissues before senescence? What is the relationship between live root respiration and FRP? Does fine root turnover (life-span) vary with soil resource availability? Measuring changes in fine root biomass alone will not provide answers to such questions. Rather, a combination of approaches must be employed.
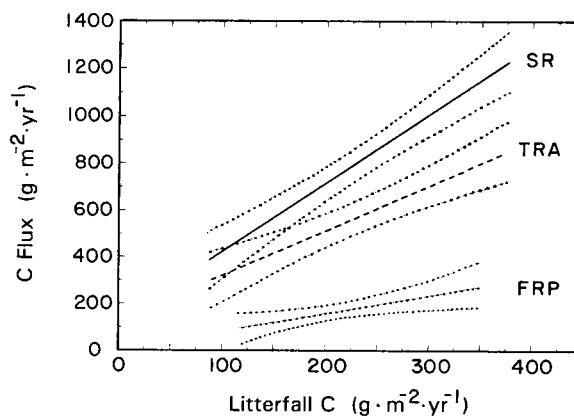

FIG. 2. Belowground carbon fluxes in relation to forest litterfall along large-scale production gradients. Predictions of soil respiration (SR) and total root allocation (TRA) are based on least squares regressions of these variables on litterfall [SR = 130 + 2.92(X) and TRA = 130 + 1.92(X), from Raich and Nadelhoffer 1989]. Fine root production (FRP) is predicted by regressing FRP estimates based on the N budget technique against litterfall (Fig. 1D). Dotted lines indicate 95% confidence regions of regressions.

Without a better understanding of the soil ecosystem, arriving at a basic understanding of controls on FRP will be difficult.

Although there is no apparent pattern in the overall data, we think it is unlikely that ecosystems or sites are unique and unpredictable with respect to patterns of above- and belowground production. Analysis of ecosystem element budgets can shed much-needed light on this problem. Often-cited high FRP estimates derived using sequential core techniques do not appear to fit within the constraints set by soil C budgets and should not be uncritically accepted. Independent analyses of forest C and N budgets both indicate that belowground production increases with aboveground production and suggest that these two components of net primary production are linked and are limited by the same factors. The global scale and the high variances in the data used in our analyses, however, argue for additional tests of patterns suggested by the element budget approach. We urge that future FRP estimates be viewed in the context of soil C budgets and, when possible, within the framework of ecosystem N budgets.

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