

MEASURING NET PRIMARY PRODUCTION IN FORESTS: CONCEPTS AND FIELD METHODS

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Abstract. There are pressing reasons for developing a better understanding of net primary production (NPP) in the world's forests. These ecosystems play a large role in the world's carbon budget, and their dynamics, which are likely to be responding to global changes in climate and atmospheric composition, have major economic implications and impacts on global biodiversity. Although there is a long history of forest NPP studies in the ecological literature, current understanding of ecosystem-level production remains limited. Forest NPP cannot be directly measured; it must be approached by indirect methods. To date, field measurements have been largely restricted to a few aspects of NPP; methods are still lacking for field assessment of others, and past studies have involved confusion about the types of measurements needed. As a result, existing field-based estimates of forest NPP are likely to be significant underestimates.

In this paper we provide a conceptual framework to guide efforts toward improved estimates of forest NPP. We define the quantity NPP* as the summed classes of organic material that should be measured or estimated in field studies for an estimate of total NPP. We discuss the above- and belowground components of NPP* and the available methods for measuring them in the field. We then assess the implications of the limitations of past studies for current understanding of NPP in forest ecosystems, discuss how field NPP* measurements can be used to complement tower-based studies of forest carbon flux, and recommend design criteria for future field studies of forest NPP.

Key words: *biomass increment; boreal, temperate, and tropical forests; carbon; coarse roots; fine root turnover; forest inventory plots; litterfall; net ecosystem C exchange; net primary production; total belowground carbon allocation.*

INTRODUCTION

An important current research need is to develop a better understanding of net primary production (NPP) in the world's forests, ecosystems that play a major role in the global carbon budget (Dixon et al. 1994). While unprecedented atmospheric concentrations (Petit et al. 1999) of the greenhouse gas carbon dioxide (CO₂) continue to increase due to anthropogenic activities, large uncertainties affect current understanding of the world's carbon budget (Melillo et al. 1996). One such uncertainty is the balance between NPP and heterotrophic respiration in forests globally. Small shifts between these fluxes can greatly affect atmospheric CO₂

concentrations. At the same time, changing climate and atmospheric chemistry (e.g., CO₂ levels, nitrogen deposition) are likely to be causing on-going changes in forest NPP. The design and evaluation of global-scale carbon models require field estimates of forest NPP and how it is responding to these global changes. In addition, a better grasp of NPP would help improve assessments of forest-level carbon (C) exchange with the atmosphere developed from eddy covariance measurements (cf. Goulden et al. 1998, Lindroth et al. 1998, Running et al. 1999). Such improvements in our understanding of forest carbon dynamics can then be used to develop better policy decisions related to forest production or conservation.

Progress in understanding NPP and its controls in forest ecosystems is hindered by the limitations of the existing field data (see recent reviews for boreal and tropical forests, respectively: Clark et al. 2001, Gower

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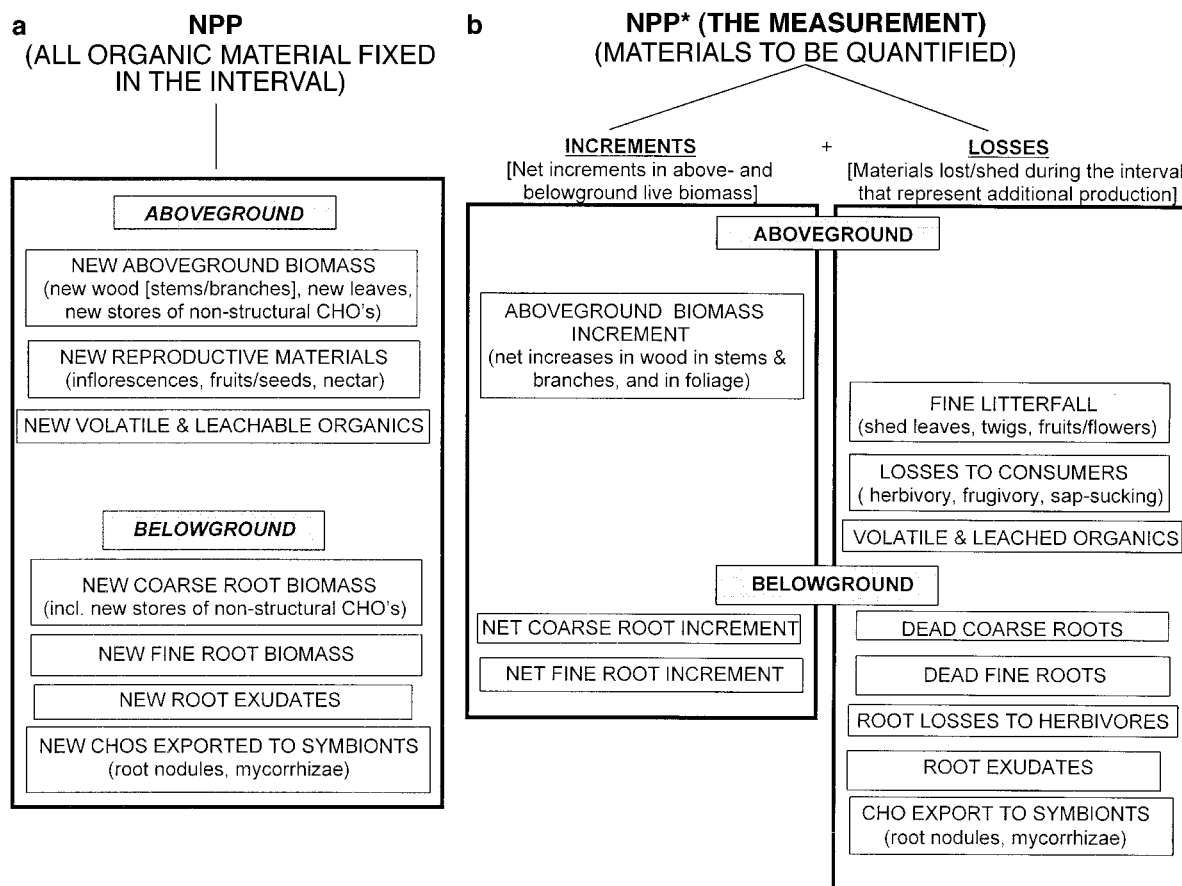


FIG. 1. The components of (a) forest NPP and (b) NPP*, the sum of all materials that together represent: (1) the amount of new organic matter that is retained by live plants at the end of the interval, and (2) the amount of organic matter that was both produced and lost by the plants during the same interval. CHO = carbohydrates.

et al. 2001). Although the ecological literature contains a plethora of papers on the topic, reported estimates of forest NPP are based on incomplete, and sometimes inappropriate, field measurements. The substantial efforts that are required for NPP field studies, the unresolved methods challenges, and a frequent lack of conceptual clarity are continuing obstacles to improving our knowledge of NPP.

In this paper we examine how forest NPP (above- and belowground) can be estimated based on field measurements. We then assess the implications of the limitations of past studies for current perceptions of the amount of NPP in forests globally, and we discuss how field NPP studies can be used to evaluate tower-based measurements of forest carbon flux. We conclude with a set of priorities and design criteria for field studies aimed at a more complete assessment of forest NPP than has been achieved to date.

ESTIMATING FOREST NPP IN THE FIELD

Net primary production is the difference between total photosynthesis (Gross Primary Production, GPP) and total plant respiration in an ecosystem. In the field,

however, it is not possible to measure forest NPP in terms of this difference (Waring and Schlesinger 1985). GPP cannot be measured directly (Ryan 1991), and estimating total plant respiration at the ecosystem level remains difficult and involves significant uncertainties (cf. Ryan et al. 1996, Lavigne et al. 1997). Alternatively, NPP is defined as the total new organic matter produced during a specified interval. Although the components of this production are readily conceptualized (Fig. 1a), they cannot be directly measured in the field because of transformations (consumption, decomposition, mortality, export) they undergo during the measurement interval. Instead, NPP must be estimated based on a suite of measurements of various types and numerous underlying assumptions. To clarify the underlying concepts and to provide a complete and internally consistent framework for field studies, we define the quantity NPP*, the field-measurement-based, operational estimate of actual NPP. NPP* (Fig. 1b) is the sum of all materials that together are equivalent to: (1) the amount of new organic matter that is retained by live plants at the end of the interval, and (2) the

amount of organic matter that was both produced and lost by the plants during the same interval.

In practice, few NPP* components are measured in field studies in forest ecosystems. Most frequently, measurements are restricted to fine litterfall and aboveground biomass increment, and their sum is considered equivalent to aboveground NPP (ANPP). Belowground components are often ignored or are estimated as some theoretical proportion of aboveground values. For example, among 48 field NPP studies in tropical forests (Clark et al. 2001: Appendix), litterfall and aboveground biomass increment were measured in 94% and 60%, respectively, of the studies; no other component of aboveground NPP* (Fig. 1b) was measured in any study, and in only 13% of the studies was any aspect of belowground production assessed. Similarly, Long and Hutchin (1991) reported that in <10% of the International Biological Programme NPP studies was any belowground biomass measured. In addition, data reported in some past NPP studies are unusable due to inadequate methods and/or inadequate documentation of methods.

Reliable assessment of the amount of forest NPP will require quantifying all materials that contribute to total NPP* (Fig. 1b), for at least a benchmark set of sites. When complete accounting is available for representative sites in each major forest type, it will be possible to identify those materials that can be ignored without producing serious underestimates of site NPP. For all NPP* components in forests, however, there are practical and theoretical challenges for obtaining accurate estimates. Further, the appropriate methods for some of them will differ among forest types. Below we review these considerations for all NPP* constituents.

Aboveground increments and losses

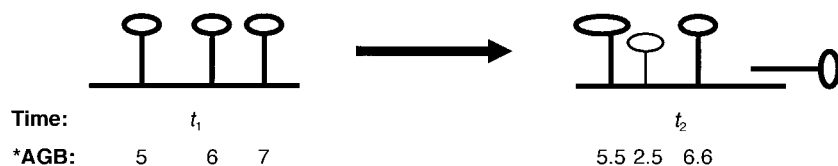
Aboveground biomass increment.—In most forest ecosystems, aboveground biomass and its increment are strongly dominated by the overstory trees. For example, it has been estimated that understory vegetation in mature moist tropical forests generally comprises <3% of the aboveground biomass (Brown 1997); given the low light levels close to the ground in these forests, the contribution by this stratum to total aboveground biomass increment is negligible. Important exceptions to this general rule are boreal forests and temperate and tropical woodlands with an open overstory and a dense ground cover or shrub layer. In such forests, where production in the understory can be substantial and may even exceed that of the trees (cf. Black et al. 1996, Gower et al. 2001), estimating total NPP requires special techniques for measurement of aboveground production by nontree vegetation. In most closed forests, however, aboveground biomass production can be reliably based on the biomass increment by trees above a carefully chosen minimum size. In large-stature forest, trees ≥ 10 cm in diameter are likely to constitute $\geq 90\%$ of vegetation biomass, and would thus suffice

for estimates of aboveground increment. In smaller stature stands such as young second-growth or tropical dry forest, a lower minimum tree size should be used and documented (cf. Murphy and Lugo 1986, Brown 1997).

Aboveground biomass increment is estimated from two successive stand-level biomass estimates. Biomass is estimated by applying harvest-based allometric regression equations to measurements of the diameters of all trees in a plot that are above the minimum size. Developing site-specific allometric equations for forest trees is laborious (harvesting one tropical emergent can require >25 person-days). Researchers therefore commonly use existing allometric equations (cf. Brown 1997, Gower et al. 1999). Because of the potential for intersite variation in factors such as tree architecture and wood density, this practice can introduce errors in estimated aboveground increment (see Gower et al. 1999). For example, Grier et al. (1984) used both site-specific and generalized regression equations to calculate foliage biomass for five *Pseudotsuga menziesii* stands, and found the generalized equations produced errors of -24 to $+93\%$. For this reason, when locally derived equations for the species under study are not available, it is important to match the allometric equation as closely as possible to the site under study (i.e., use an equation based on data from one or more sites of comparable climatic and edaphic conditions), or, preferably, to test its predictions by first measuring and then harvesting individual trees or forest plots on site.

Two approaches (Fig. 2) can then be used for estimating aboveground biomass increment from field measurements and biomass allometry. Both approaches give the same estimated aboveground biomass increment, although tree mortality and ingrowth (trees that grew past the minimum diameter during the interval) have to be accounted for differently in the two cases. Not understanding the subtleties between these two methods can lead to erroneous estimates of aboveground biomass increment and thus ANPP or total NPP.

Approach 1 is based on tracking individual trees. The increment for each tree is calculated as the difference between its estimated biomass at the beginning and end of the interval. If a tree dies in the measurement interval and the intercensus interval is short, the tree can be assumed to have no increment and is ignored in the calculation (but see Approach 2). Thus, for the stand, increments are summed for all trees surviving the interval. This total is then adjusted for ingrowth; the increment of each new tree is calculated as the difference between its estimated biomass at the end of the interval and the biomass of a tree of the minimum measured diameter. The summed increments of the ingrowth are then added to the stand increment. A variant of this approach, but with the same calculation methods (Approach 1, Fig. 2), can be used in forests where the trees make reliable annual rings. All the live trees in a plot are cored, the annual rings they formed over the

**Approach 1:**

$$\begin{aligned} \text{Stand Increment} &= (\Sigma \text{ Increments of surviving trees}) + (\Sigma \text{ Increments(s) of ingrowth}) \\ &= ((5.5 - 5.0) + (6.6 - 6.0)) + (2.5 - 2.0) \\ &= (0.5 + 0.6) + (0.5) \end{aligned}$$

Approach 2:

$$\begin{aligned} \text{Stand Increment} &= (\Sigma \text{ AGB at } t_2 - \Sigma \text{ AGB at } t_1) + (\Sigma \text{ Biomass of trees that died in the} \\ &\quad \text{interval}) - [(\text{Biomass of a minimum size tree}) \times (\text{number of new trees})] \\ &= ((5.5 + 2.5 + 6.6) - (5 + 6 + 7)) + (7) - (2 \times 1) \\ &= (14.6 - 18.0) + (7) - (2) \\ &= 1.6 \end{aligned}$$

FIG. 2. The two methods for calculating aboveground biomass increment based on measurement of all trees in a plot at the beginning and end of an interval. Approach 1 is based on tracking individual surviving trees. Approach 2 is based on measuring all trees in the stand at each census but also requires measurement of trees (a) that died in the interval and (b) that recruited past the minimum size during the interval. AGB = aboveground biomass of live trees; AGB of a minimum-sized tree is set at 2 units.

interval of interest are measured, and these radial increments are then converted to biomass increments using the allometric equation.

In Approach 2 (Fig. 2), the estimated total aboveground biomass of the stand at the beginning of the interval is subtracted from the estimated total aboveground biomass of the stand at the end of the interval, with no reference to increments of individual trees. This difference then has to be adjusted for both tree mortality and ingrowth. For the mortality correction, the biomass of all trees that died during the interval is estimated from their initial diameters and added to the net change in stand biomass. If the measurement interval is long (>2 yr), attempts should be made to estimate the within-interval growth by all trees that died; failure to do this will produce an underestimate of stand increment, especially when large trees died during a many-year interval. To correct for ingrowth, the number of new trees is multiplied by the biomass of the minimum-diameter tree being measured (see Approach 1), and this product is subtracted from the mortality-adjusted stand increment.

Approach 2 is often used to calculate aboveground biomass increment from large-scale forest inventory data (e.g., Schulze et al. 1999) or for stands that are remeasured after a long interval (e.g., 35 yr, Weaver and Murphy 1990). Failing to make the corrections for tree mortality when using Approach 2 will result in underestimating the aboveground biomass increment by an amount at least equal to the initial biomass of trees that died in the interval (see above). In tropical forests, for example, because stand-level mortality of trees ≥ 10 cm in diameter is usually 1–3% of stems per

year and is independent of tree size (Swaine et al. 1987, Hartshorn 1990), the underestimate caused by not accounting for dead trees will average ~ 1 –3% of the initial aboveground biomass per year of census interval (as found by Carey et al. 1994). Within-interval growth of the trees that died in the interval would augment this error. Similarly, in temperate zone plantations or successional forests with high tree mortality due to thinning, either natural or anthropogenic, the “missing” biomass from trees that died in the interval could be very large. Thus, failing to correct for tree mortality when using Approach 2 (e.g., Weaver and Murphy 1990) can produce a substantial underestimate of NPP. It will also have a high variance, especially in areas affected by catastrophic disturbance (hurricanes, landslides), and in small study plots, where not accounting for the death of one very large tree could result in a severe underestimate of aboveground increment. For many published estimates of aboveground increment from both boreal and tropical forests, it is not possible to judge the reliability of the estimates because the authors failed to state how they dealt with mortality (see Clark et al. 2001, Gower et al. 2001).

Even when the biomass accounting is carried out correctly, several other sources of error can affect estimates of aboveground biomass increment. One is over- or underestimating the biomass of very large trees (arbitrarily defined as those of diameters > 70 cm). In tropical forests, for example, although densities of such trees are low (usually $< 10\%$ of stems ≥ 10 cm in diameter), they can comprise 25–50% of the total aboveground biomass (Brown and Lugo 1992, Brown et al. 1995, Clark and Clark 1996). If the biomass allometry

equation is based on harvest data that do not cover the largest tree sizes, the biomass estimates for out-of-range big trees may be highly inaccurate (Brown and Lugo 1992, Brown et al. 1995).

Another potential source of error in estimating aboveground biomass increment is the progressive loss of trees' biomass through heartrot and branchfall (self-pruning, wind, and lightning damage). If the allometric equations were based on harvesting a representative sample of trees of all sizes, including those that have lost mass due to such factors, the resulting estimate of biomass increment will need to be "corrected" for these woody biomass losses due to a question of mass balance. The difference in a tree's initial and final biomass over an interval is the net result of the production of new biomass and the loss during the interval of both new and old (previously produced) woody material due to processes such as branchfall, crown damage by storms, and heartrot. When substantial woody mass is lost by trees during the interval, and when the biomass allometry is based on representative trees, including those with such losses, the true production of new aboveground biomass in the interval will be underestimated by allometry unless the lost mass is added back to the final estimated biomass. The largest mass loss in most forests is usually branchfall. Estimates of branchfall (wood >1 cm in diameter) in 10 tropical forest sites ranged from 0.1 to 2.9 Mg C·ha⁻¹·yr⁻¹ (Clark et al. 2001). Because branchfall can be highly variable from year to year, continuous measurements over 5–10 yr would likely be needed for a reliable "background" rate of branchfall for this correction. Also, branches fallen from standing dead trees would need to be identified and excluded from the measurements of branchfall mass. If, however, the allometric equations are based on the harvest of less damaged trees, adjusting the estimated biomass increment for these types of mass loss would be incorrect.

With long intercensus periods (e.g., 13 yr, Lieberman et al. 1990; 35 yr, Weaver and Murphy 1990), aboveground increment will be underestimated if ingrowth is not considered. Small trees may have grown past the minimum diameter and then died before the remeasurement. The impact of missing such trees will depend on stand structure. In large-stature forest, the ingrowth of small trees may have a negligible effect on estimates of aboveground increment.

Several additional factors affect the estimation of aboveground increment in tropical forests. The height of diameter measurement should be above the buttresses and other bole irregularities that commonly occur on large tropical trees at breast height (dbh = 1.30–1.37 m above the ground). The allometric equations (cf. Brown 1997) relate tree biomass to the cylindrical bole diameter, which is much smaller than the diameter at breast height on buttressed trees. Increments based on around-buttress measurements will be inflated, both because of misapplication of the allometry, and be-

cause of the faster radial growth of these stem irregularities (cf. Sheil 1995). Second, with the high species diversity of tropical forests, it is not feasible to develop species-level allometries that can be used for estimating stand-level biomass increment. Given the wide range of wood densities and tree architectures present in a single tropical forest stand, the development of a single biomass allometry equation for such forest should be based on sampling large numbers of trees of all sizes and conditions. Nevertheless, despite the limited tree biomass data from different tropical forests, pooling the data across species and grouping them by broad climatic zones produces highly significant regression equations with >90% of the variation in tree biomass explained by diameter alone (Brown 1997). How well the existing tropical allometry equations predict stand biomass has been practically untested. To do this would require comparing the predicted and measured biomass of independent samples of trees harvested on site or in that forest type. In one recent study (Araujo et al. 1999), the actual fresh biomass of a harvested Amazonian forest plot was compared to predictions from 14 allometric equations developed elsewhere in Amazonia; although some of the equations predicted biomass well, others produced highly erroneous estimates (up to 318% higher than actual biomass). Additional sources of error in tropical forests are the atypical allometry and growth patterns of three large woody growth forms: palms, hemiepiphytes, and lianas. Palms, which can be up to 25% of the stems ≥10 cm in diameter in tropical forests (e.g., Lieberman et al. 1985), differ from the other trees in biomass allometry (Brown 1997), and most of their growth is apical. Hemiepiphytes (shrubs and trees) also have distinctive allometries, and they can attain large sizes and densities in some tropical forests. Similarly, lianas, which can account for 30% of canopy leaf area in tropical forests (Putz 1984), strongly contrast with trees in both their biomass allometry (Putz 1983) and the way they grow (principally by stem elongation; Putz 1990). Applying tree biomass allometric equations to these growth forms could produce erroneous estimates of biomass increment. Also, lianas and hemiepiphytes are missed when their stems do not descend to near the ground within the plot. The degree to which these growth forms distort estimates of tropical forest biomass increment is unknown.

Special consideration is also needed for forests that are completely deciduous, such as many temperate and boreal hardwood forests. For these, the aboveground biomass increment should be estimated from biomass allometric equations that exclude foliage mass. This will eliminate the possibility of including the same foliage twice in NPP*, by estimating it both from leaf litterfall and as included in aboveground increment.

Aboveground losses.—In addition to the accumulation of new biomass by plants, some of the organic matter produced in an interval is shed or otherwise lost by plants during the interval. Such losses include

leaves, flowers, fruits, material lost to herbivores, biogenic volatile organic compounds, and leached organics (Fig. 1b). These materials are not considered in measurements of biomass increment and need to be added to it for an estimate of aboveground NPP.

1. *Fine litterfall*.—Although any net increase in live leaf biomass is accounted for as part of the aboveground biomass increment (except in strictly deciduous forest [see *Aboveground increments and losses: Aboveground biomass increment*]), a large additional fraction of current-interval leaf production, along with other short-lived plant material such as flowers and twigs, will be shed before the end of a measurement interval. Fine litterfall is one of the largest components of NPP* and is the most frequently measured in many types of forest. Relatively straightforward to measure directly, fine litterfall nevertheless presents special challenges.

A nontrivial issue is which material to collect. While the goal is clear, to quantify all the current interval's new organic matter that is shed by plants aboveground (Fig. 1b), doing this correctly is not as simple as it appears. Clearly appropriate components are fallen leaves and plant reproductive parts. Because large fallen branches are mostly composed of wood produced in years prior to the measurement interval, they should be excluded from fine litterfall (but see *Aboveground biomass increment*). Even small fallen twigs are a mix of organic matter fixed in the current year and in previous years. An upper size limit must be set on the woody material considered as part of fine litterfall. A reasonable upper bound is a diameter of 1 cm. (At a diameter growth rate of 2 mm/yr, most cross-sectional area (64%) of a 0.5 cm diameter twig will be from the current year's growth.)

Unfortunately, as documented for tropical forests by Proctor (1983), NPP studies have been notoriously non-standardized with regard to woody "fine litterfall". In numerous studies, all size ranges of woody material, including the largest branches, have been counted as litterfall, and in others a variety of maximum diameters have been used (Clark et al. 2001). This problem is compounded by the fact that authors frequently report litterfall values without specifying what material was collected.

A second issue is leaf longevity. To the degree that leaves live >1 yr, annual leaf litterfall will include production from both the current and past years. In most cases, all this material should be included in NPP* due to mass balance considerations. The difference between a tree's live foliage mass at the beginning and at the end of an interval is the net result of new foliage production during the interval, and loss during the interval of both new and old (previously produced) leaves. To account for the total new foliage production during the measurement interval, the "old" and "new" leaves in fine litterfall need to be added to the net live foliage increment (the foliar portion of aboveground biomass increment). However, under some conditions,

such as an extreme drought that causes anomalous leaf drop and a net loss of live canopy foliage, leaf litterfall could include inappropriate material that would inflate the estimate of current-year foliar NPP. Such an occurrence could invalidate field estimates of current-year NPP or of interannual variation in NPP. To develop reliable estimates of fine litterfall, this material should be measured over several years.

The timing and frequency required for litterfall collection will depend on several factors. Although litterfall may be very reduced during the leaf-off season in some deciduous forests, fine litterfall estimates should be based on continuous collection through the year. In many forest types, high rainfall and temperatures during at least part of the year make it necessary either (1) to collect litterfall at least every two weeks to avoid significant losses due to decomposition (cf. Stocker et al. 1995), or (2) to measure decomposition rates and back-correct the litterfall biomass accordingly. In wet tropical forest in New Guinea, for example, Edwards (1977) estimated that twigs <1 cm in diameter lost 36–40% of dry mass before falling into the litter traps. Similarly, Frangi and Lugo (1985) suspended large, old leaves from palms in Puerto Rico and found about half their mass was lost through decomposition before they fell.

In all forests, the estimation of fine litterfall can be highly uncertain due to the use of insufficient numbers of traps to deal with the high intertrap variance in collected material. Field studies should be based on pre-sampling to quantify this variance and to define the necessary number of traps. Secondly, confidence intervals should be given for any reported litter data.

In tropical forests, "fine litterfall" often includes large items such as 10-m-long palm leaves. Nonstandard approaches to littertrap design and management are needed to sample these adequately; otherwise, fine litterfall can be severely underestimated (Villega and Proctor 1999). A second, unquantified cause of litterfall underestimation in tropical forests is that leaves and other fine litter are often trapped in the crowns of other plants (palms, understory shrubs), where they are consumed or decompose. As a result, this component of litterfall is never collected in littertraps.

2. *Aboveground losses to consumers*.—Aboveground production can be subject to substantial losses to consumers, at least in some forest types and at some times (e.g., insect outbreaks). Not accounting for leaf herbivory and seed and fruit predation may result in underestimates of NPP. Additional production is also lost to sap-sucking insects and nectarivores.

Of these classes of consumption, only herbivory has been quantified in forest NPP studies, and only in a small proportion of them. Several studies (cited in Lowman 1995) have shown that grazers can consume as much as 12–30% of leaf biomass. When herbivory is estimated from the percentage of the area missing from leaves collected in littertraps (e.g., Odum and

Ruiz-Reyes 1970, Edwards 1977), it is underestimated, because this method misses the losses of entire leaves to herbivores. When this method was used concurrently with studies of individually tracked leaves (a subtropical Australian forest [Lowman 1984], a Mexican tropical dry forest [Filip et al. 1995]), the estimated losses based on instantaneous area measurements were only about half those based on tracking leaves (Australia: 8 vs. 15% area lost per year; Mexico: 8 vs. 17% area lost per year). Thus, leaf herbivory should ideally be assessed on site by the latter method, and the estimated loss should be used to back-correct the leaf components of fine litterfall and aboveground biomass increment.

Similarly, predispersal consumption of fruits and seeds reduces the biomass of these materials before they reach littertraps, and animals can also remove these materials from the traps. Not accounting for these losses may produce an underestimate of NPP. For example, fruit production of the dominant plant species in a Puerto Rican palm forest was estimated in a separate study to be 14 times the fruit fall measured in litter traps (Lugo and Frangi 1993). Janzen and Vázquez-Yanes (1991) have estimated that, for nearly all tropical trees, >50% of seeds are lost to animal consumers or fungi. In temperate and boreal forests, pre-collection losses of reproductive material may be considerably less, but this needs to be demonstrated. Study of the relationship between actual production of seeds, fruits, and flowers, and collections from litter traps is needed in all forest types, so that NPP* can be corrected appropriately.

3. *Biogenic volatile organic compounds and leached organics.*—It is not yet known what proportion of forest NPP are biogenic volatile organic compounds (BVOCs), compounds with important effects on atmospheric chemistry (Crutzen et al. 1999). Using the available emissions data and estimates of biome-specific factors such as foliar density and climatic variation in emissions, Guenther et al. (1995) modeled global BVOC fluxes. Their model projected that “tropical woodlands” (rain forest, seasonal, drought-deciduous, and savanna) produce nearly half of total world BVOC emissions. Combined emissions of isoprene, monoterpenes, and other reactive volatile organic compounds were estimated to be 0.31, 0.15, and 0.21 Mg C·ha⁻¹·yr⁻¹ for tropical rain forests, tropical montane forests, and tropical seasonal forests, respectively. For boreal conifer forest, in contrast, they estimated combined emissions to be <0.02 Mg C·ha⁻¹·yr⁻¹. These estimates suggest that BVOCs are an insignificant proportion of forest NPP. However, Guenther et al. (1995) underlined the uncertainties in these first-order calculations due to the few data and limited understanding of underlying processes. They estimated the uncertainty around the tropical emissions to exceed a factor of three. Furthermore, BVOC emissions increase with temperature (Lerdau and Keller 1997, Constable et al.

1999) and may be responding strongly to the global temperature increase.

A second component of aboveground NPP* (Fig. 1b) that remains unquantified for forests is the leaching of organics from aboveground plant parts. Studies of cultivars suggest that such losses in throughfall may not be negligible (0.8 Mg·ha⁻¹·yr⁻¹ of organic leachates in apple orchards [Dalbro 1955]; 6% of carbohydrates leached from young bean leaves in 24 h [Tukey and Mecklenburg 1964]).

Belowground increments and losses

Belowground production in forests remains poorly understood due to method challenges and incomplete measurements. There are seven components of belowground NPP* in forests (Fig. 1b): biomass increments in coarse roots and in fine roots, mortality losses of new coarse root and fine root production, losses of root material to belowground consumers, rhizodeposition (root exudates, sloughed root cells, etc.), and the carbohydrate inputs to mycorrhizal fungi and root nodule symbionts. There are no straightforward methods for field measurement of any of these components. However, there are some promising new directions for quantifying belowground NPP.

A first need is to define “coarse” and “fine roots.” Fine roots are considered the most biologically active and show rapid turnover while usually contributing little to total root biomass in old-growth forest (Vogt et al. 1996, Cairns et al. 1997). They are thought to account for a large portion of total annual losses of organic material in most ecosystems. Large roots, in contrast, are thought to turn over slowly, and their contribution to NPP is largely in terms of biomass increment. The operational distinction between coarse and fine roots varies across studies, and it will be highly desirable to standardize this. Regardless of the limit used, however, the critical point for NPP studies is to cover the entire size range of roots.

Belowground biomass increment.—

1. *Net coarse root increment.*—For direct field measurement of this NPP* component, two kinds of information are needed: the standing biomass and size distribution of coarse roots in the study plot, and their size-dependent increments. Developing reliable estimates for either of these is problematic in any forest. The best estimates of coarse root biomass will come from a two-pronged effort (Bledsoe et al. 1999) that combines: (1) sampling of coarse roots in replicated monoliths in the areas away from tree stems, and (2) a biomass allometry approach based on excavation and harvesting individual trees' coarse root systems within a given radius of the stem and relating them to tree diameter. Then, the tree diameter distribution in a study plot and the monolith data can be combined to estimate the standing crop of coarse roots. Backhoes and fire trucks have been used to excavate the coarse roots of trees in plantations and forest in the temperate and

boreal regions (Bledsoe et al. 1999). In tropical forests, where root systems have been excavated for only a handful of individual trees (see Clark et al. 2001), reliable estimates of the allometry between coarse root biomass and aboveground tree biomass await a greatly expanded database; this will likely be built up slowly and opportunistically (relying on recently cut soil profiles along roadsides).

Techniques still need to be worked out for directly measuring radial and longitudinal growth rates of the different sizes of coarse roots. To date, stand-level coarse root increment has been estimated based on the diameter distributions and increments of the trees and allometric relations between root biomass and aboveground tree biomass. A potential problem with this indirect method is that the smallest roots commonly classified as "coarse roots" (often 2–10 mm in diameter) are unlikely to be well characterized in biomass allometric approaches because of breakage and incomplete sampling in excavations of root systems; these small, coarse roots may be considerably more dynamic (i.e., account for more NPP*) than larger roots.

2. *Net fine root increment.*—This NPP* component is any net increase in live fine root biomass during the measurement interval. To measure this fraction of belowground production would require quantifying initial and final biomass of live fine roots. Methods for assessing standing stocks of fine roots are discussed below.

Belowground losses.—

1. *Dead coarse roots.*—The same mass balance considerations that affect estimates of foliar NPP apply to estimating the production of coarse roots; both coarse root increment (see *Net coarse root increment*) and coarse root mortality need to be quantified. The techniques needed to measure standing stocks of dead coarse roots are the same as those needed for assessing live coarse root biomass. To estimate coarse root mortality over a measurement interval (Fig. 1b) requires estimating the net change in the stocks of dead coarse roots; decomposition of these larger roots is unlikely to be a big source of error.

2. *Dead fine roots.*—Fine root losses and even fine root standing stocks are difficult to measure in forests (see Bledsoe et al. 1999, Fahey et al. 1999). Estimates of standing stocks of fine roots are highly uncertain due to the notorious temporal and spatial variability in fine root biomass (e.g., Carvalheiro and Nepstad 1996, Ostertag 1998). Second, particularly in strongly seasonal tropical forests, live roots can occur much deeper in the soil profile than has been assumed (e.g., to 18 m depth in an eastern Amazonian forest [Nepstad et al. 1994; see also Trumbore et al. 1995]). These factors, along with the challenge of distinguishing live from dead fine roots, make it difficult to assess fine root dynamics. Techniques that sample only the top of the soil profile can underestimate fine root production and mortality. Peak fine root biomass cannot be used as a

surrogate for annual production, given the potential for year-round belowground production and mortality. Sequential coring methods based on simply summing statistically significant increments in fine-root biomass between sampling periods would lead to underestimates in those forests where root production and mortality co-occur (even if total fine root stocks are unchanging). Such errors are compounded when temporal patterns of fine root production and mortality differ among soil depths, as found in northern hardwood forest by Hendrick and Pregitzer (1996).

In spite of the challenges, assessment of fine root dynamics should receive high priority, given the potentially large fraction of NPP that can be involved (cf. an estimated 32–49% in two classes of Alaskan taiga forests [Ruess et al. 1996]). Because all currently available methods have problems associated with them, current consensus (see Vogt et al. 1998, Fahey et al. 1999) is that the most robust direct estimates will come from using multiple techniques in parallel, and cross-checking results between them. The most promising methods combination appears to be (1) the compartment model approach to sequential coring (Fairley and Alexander 1985, Santantonio and Grace 1987, Publicover and Vogt 1993), and (2) minirhizotrons (cf. Aerts et al. 1989, Steele et al. 1997, Fahey et al. 1999). The compartment model method combines repeated destructive sampling to assess standing stocks of live and dead fine roots, with in situ measurement of fine root decomposition under differing environmental conditions (e.g., soil moisture, temperature). A simple flow model can then be used to estimate the biomass of fine roots produced and lost during the intervals between samples, based on the mass of live and dead roots in successive samples and on the climatic conditions for decomposition in each interval. The minirhizotron approach, based on sequential video images taken from within a buried transparent tube, enables direct observation of the production and mortality of fine roots, at differing depths in the soil profile. However, this technique is extremely labor intensive and may be hard to replicate sufficiently to deal with the spatial variability in fine root biomass. It involves soil disturbances on installation that could affect root behavior (although intense biotic soil-mixing in some forests likely restores soil structure within a few months). Using minirhizotrons to estimate fine root production also requires data on fine root biomass. The data on root growth and mortality are based on root length, and relationships between length and biomass are needed to convert measurements to biomass. The demographic data provided by minirhizotrons can be critical, however, because erroneous estimates of fine root life-span will produce large errors in estimates of fine root production. In the absence of direct data, some past estimates of belowground carbon cycling (cf. Trumbore et al. 1995) have been based on the assumption that fine roots turn over annually. A number of recent minirhizotron studies

have shown, however, that tree fine roots can have much shorter life-spans (e.g., 85 d in an oak forest in Spain, Lopez et al. 1998; 15–180 d in 10 of 14 studies of temperate forest trees reviewed by Eissenstat and Yanai 1997; <14 d for >40% of *Prunus avium* roots, Black et al. 1998); with such short life-spans, fine roots would account for considerably more NPP than would be estimated based on a 1-yr life-span. In contrast, where mean fine root longevities are found to be much greater than 1 yr, assuming a 1-yr life-span would result in overestimating the carbon allocation to fine root production.

3. *Rhizodeposition, inputs to symbionts, and root losses to consumers.*—Recent studies have indicated that these three belowground processes may account for a large proportion of total NPP in forests. Rhizodeposition (soluble root exudates, mucilaginous material, sloughed root cells, etc. [Darrah 1996]) and export to mycorrhizae were estimated to represent >30% of NPP for ponderosa pine seedlings (Norton et al. 1990). In a mature fir stand, carbon allocation to mycorrhizae was estimated at 15% of forest NPP (Vogt et al. 1982). Bekku et al. (1997) found root exudates to account for 3–13% of NPP for temperate weed seedlings. Rhizodeposition is as yet unquantified at the forest level. Similarly unknown is the amount of new root biomass that is consumed by soil organisms. Eissenstat and Yanai (1997) have recently argued that root herbivory is likely to be much greater than is generally appreciated, given the lack of structural defenses in young roots.

Constraining belowground NPP.—Given the challenges for measuring the components of belowground NPP*, an indirect method based on carbon mass balance (Raich and Nadelhoffer 1989) can be used to constrain estimates of total belowground NPP. An upper bound for total BNPP can be estimated by subtracting the carbon input to the soil by aboveground litterfall from that emitted in soil respiration. Total soil respiration comprises: (1) root respiration, (2) respiration by microbes decomposing the litter and other materials shed by plants both above- and belowground, and (3) a minor level of respiration by other soil organisms. If soil organic carbon (SOC) is close to steady state, if fine root biomass and coarse root biomass are also close to steady state, and if fine litterfall is the only significant aboveground source of carbon, then subtracting the litterfall carbon from the carbon respired from the soil provides an estimate of total belowground carbon allocation by the plants (TBCA). TBCA is the summed carbon in root respiration plus all belowground components of NPP (Fig. 1a). Neglected in this calculation, however, are several potential aboveground carbon sources in forests: decomposing coarse woody debris, leached organics from aboveground vegetation, dead animals and frass, and carbon in dry and wet deposition. If any of these is significant, their omission will inflate estimated TBCA. The estimate of TBCA is thus

a high upper bound for total belowground NPP under steady-state conditions. When concurrent data on annual litterfall and annual soil respiration are available, this method should be used to check the plausibility of field estimates of belowground components of NPP* (cf. Nadelhoffer et al. 1998). Multiple issues arise with respect to interpretation, however.

One important uncertainty is the magnitude of root respiration. Some have assumed it to account for ~50% of TBCA (cf. Raich et al. 1991). In two recent studies in temperate deciduous forests, however, root respiration was estimated to be 33% (Bowden et al. 1993) and 90% (Thierron and Laudelout 1996) of soil respiration. Using the C-balance method in eastern Amazonia, Trumbore et al. (1995) estimated root respiration to be 50–65% of soil respiration. This estimate was based on the assumption that the carbon in the standing stocks of fine roots (<1 mm in diameter) equaled the total belowground carbon input by plants to the soil over an annual cycle. Including faster fine root turnover, losses of roots ≥ 1 mm in diameter, or rhizodeposition would have decreased their estimate of root respiration. Unfortunately, estimating forest-level root respiration by more direct methods is made difficult by potential measurement artifacts (cf. Clinton and Vose 1999) and the high spatio-temporal variation of root biomass.

A second issue arising with the C-balance method is its requirement that SOC be close to steady state (Nadelhoffer et al. 1998). This assumption may be violated in today's forests, given that forest soils contain large quantities of SOC (Dixon et al. 1994, Schlesinger 1997) that can be very dynamic (cf. Davidson and Trumbore 1995, Binkley and Resh 1999), and given that SOC turnover increases with temperature (Trumbore et al. 1996, Goulden et al. 1998, Lindroth et al. 1998), and that global temperatures are increasing. Resulting errors, however, will be conservative when TBCA is taken as an upper bound for BNPP, because efflux of old SOC in soil respiration will inflate the TBCA estimate. Two other potential non-steady-state processes, however, would have the opposite effect: net C losses from the soil profile as dissolved organic carbon, or any net accumulation of SOC. If either of these occur at nontrivial rates, they would need to be factored into the C-balance calculation.

Given the potential impacts of year-to-year climatic variation and of local to large-scale disturbances on forest production (cf. Schulze et al. 1999), root dynamics are likely to vary among years. Applying the C-balance method in forest NPP studies will therefore be most useful when based on multiple years of concurrent litterfall and soil respiration measurements that are well replicated within the study area, thus averaging out the spatiotemporal variation in these two fluxes. Finally, when estimated TBCA is compared across sites and studies, careful attention needs to be given to the litterfall methods in each study. The great variation in

litterfall definitions and methods in past NPP studies (see *Aboveground losses: Fine litterfall*) could produce spurious inter-site differences in BNPP as estimated by the C-balance method.

New Stored Nonstructural Carbohydrates

Some net primary production can be allocated to storage by trees both above- and belowground in the form of nonstructural carbohydrates. As noted by Waring and Schlesinger (1985), any significant stand-level changes from year to year in the amount of such storage will provide problems for the estimation of total NPP. This issue has not yet been addressed in field studies of forest NPP.

SCALING ISSUES

In addition to the lack of direct measurements of many NPP* components, plot biases and a lack of replication in space and time decrease the reliability of existing estimates of forest NPP. Within the boreal region, the fire-disturbance cycle (Price and Apps 1996, Schulze et al. 1999) has pervasive effects on forest carbon dynamics. Tropical moist forests have strong spatial variation in forest structure and edaphic conditions at the local scale (cf. Richter and Babbar 1991, Clark et al. 1998, Laurance et al. 1999), and are likely to show corresponding within-forest variation in productivity. For example, Gower (1987) found a doubling of fine root biomass between two soil types in one small area of lowland forest in Costa Rica. The small study plots generally used for ecological studies in these forests often have an over-representation of large trees (Brown and Lugo 1992, Brown 1997) and show high interplot variance in total aboveground biomass due to the spotty distributions of the large trees (Brown et al. 1995). To assess NPP in such internally heterogeneous forests, measurements should be replicated in space, ideally in a stratified random fashion with respect to the major gradients of within-forest variation. Similarly, NPP* components in a given forest can show substantial temporal changes due to interannual climatic variation, as has been found for aboveground biomass increment in boreal forest (Yarie 1997) and for tree growth rates in tropical wet forest (Clark and Clark 1994). For a robust assessment of NPP in a given forest, measurements should be made over multiple yearly cycles.

UNDERESTIMATION OF NPP IN FIELD STUDIES

Given the uncertainties and the incomplete measurements characterizing forest NPP studies to date (see Clark et al. 2001, Gower et al. 2001), we can only make educated guesses about the impact of frequently used procedures on estimates of total NPP. To illustrate the issues and their potential relative importance, however, we have developed error estimates (Table 1) for one example site, a tropical moist forest (Khao Chong, Thailand) for which Clark et al. (2001) have estimated

total NPP (lower bound) to be $11.8 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, based on the existing field data (aboveground biomass and aboveground biomass increment [Kira et al. 1967]) and additional NPP components estimated by Clark et al. (2001). We emphasize that this exercise is heuristic in intent. As detailed in Table 1, it involves many arbitrary assumptions and builds on fragmentary data from other studies. It does, however, provide insights into the uncertainty associated with existing field methods for estimating NPP.

The first conclusion that can be made from this exercise (Table 1) is that, at any study site, some of the methodological issues will be particular to the forest type being studied (e.g., the potential for double-accounting foliage production in deciduous forests, large palm leaves skewing litter estimates in tropical forests, and the large contribution of NPP from ground cover or the shrub layer in some boreal forests). Thus, field methods need to be carefully adjusted to the conditions of the site; failing to do this can produce major errors in estimated NPP. Second, the relative impact of some of the more general methods issues can vary among forest types. For example, precollection decomposition is likely to most strongly affect fine litterfall estimates in the warm, humid conditions of tropical moist and wet forest. In forests with higher root:shoot ratios, belowground methods issues may have higher relative impacts on NPP estimates. Third, and most important, most of the procedural problems in NPP field studies result in underestimating NPP. Some of these can individually produce large underestimates of NPP. Summed, the error estimates in Table 1 suggest the potential for underestimating NPP by $>200\%$ in this forest. Neglecting NPP* components accounts for most of this potential underestimation, followed by errors associated with measuring aboveground increment and fine litterfall.

Most forest NPP studies involve an important number of these errors and omissions. For example, in their recent review of field NPP* data in boreal forests, Gower et al. (2001) found that even the most complete studies failed to assess carbon allocation to mycorrhizae, and that fine root production and foliar herbivory were usually also not measured. Further, no study included estimates of root exudates, root herbivory, BVOC production, losses of organic leachates, seed consumption, or losses to sap-suckers. With the exception of fine root production, this same list of NPP* components as well as fine litterfall were all unmeasured in the classic study of 40-yr-old Douglas fir stands by Keyes and Grier (1981) that focused on how ANPP and BNPP change with differing site productivity. Similarly, in our review of the existing field NPP* data for tropical forests, we found that all studies involved many of the omissions and methods problems noted in Table 1 (see Clark et al. 2001). Thus, in addition to the uncertainty around most NPP numbers due to sampling issues, the field research to date appears

TABLE 1. Estimated potential impact of problems associated with common procedures in field measurements of NPP* components, for a case study site in tropical moist forest (Khao Chong, Thailand).

| Procedure | Potential impact on estimated NPP* (% of NPP* estimate) |
|---|---|
| Aboveground increment | |
| Using an inappropriate biomass allometry developed off site | -20 to +11% |
| Applying the tropical moist forest equation (Brown 1997) to a tropical wet forest (Clark and Clark 2000) produced a 79% increase in estimated aboveground biomass compared to that from the tropical wet forest equation (Brown 1997). We assume this level of impact on estimated biomass (either increase or decrease), and a proportional effect on aboveground increment. | |
| Not correcting for tree mortality (Approach 2) | -25% |
| We assume (see text) that annual biomass loss through tree mortality = 2% of aboveground biomass (= 3.3 Mg C·ha ⁻¹ ·yr ⁻¹). This reduces the (correctly) measured aboveground increment (3.0 Mg C·ha ⁻¹ ·yr ⁻¹) to 0. | |
| Not accounting for growth of trees that died in the interval | -3 to -0.3% |
| We assume that trees that die contribute 1% of the aboveground biomass increment per year during the intercensal interval, given that tree mortality in tropical forests averages 1-3% (see <i>Aboveground increments and losses: Aboveground biomass increment</i>). The estimate error range is for census intervals of 1-10 yr. | |
| Not accounting for ingrowth | -1% |
| We assume that the percentage of new stems = the percentage of dead stems (both 2%), that stem density is 500 trees (≥10-cm diameter) per hectare, and that the biomass increment of a new tree is 29 kg (the difference between a tree of 12-cm diameter and that of the minimum-sized tree, at 10-cm diameter), per the tropical moist forest allometric equation of Brown (1997). | |
| Using an allometry based on harvest data that do not cover the larger tree sizes | -3 to +6% |
| We assume that harvested trees underlying the allometry were all ≤70-cm diameter, that 25% of total stand biomass (167 Mg C/ha; Kira et al. 1967) is in larger trees, that biomass increment is proportional to biomass, and that the error in projected biomass of the out-of-range trees can be from -50% to +100%, depending on the allometric equation used. | |
| Not correcting for branchfall and heartrot | -17 to 0% |
| We assume that the long-term average mass loss through branchfall and heartrot by surviving trees is 2.0 Mg C·ha ⁻¹ ·yr ⁻¹ . This material needs to be counted as NPP* (a mass balance correction) when the biomass allometry is based on representative trees; no correction should be made when the allometry is based on unrepresentative (undamaged) trees. | |
| Applying the tree biomass allometry equation to palms, lianas, and hemiepiphytes | ??? |
| There is currently no basis for estimating the errors due to these life forms (see <i>Aboveground increments and losses: Aboveground biomass increment</i>). | |
| Not measuring the lianas and hemiepiphytic trees and shrubs that do not extend down to ground level | -3 to 0% |
| We assume such stems account for a maximum of 10% of the total aboveground biomass increment. | |
| Fine litterfall | |
| Not correcting for decomposition before material falls in traps | -12% |
| We assume that small wood and leaves are 5.6 Mg C·ha ⁻¹ ·yr ⁻¹ (95% of fine litter), and that they average a 20% mass loss from decomposition before being collected in traps. | |
| Including large wood (>1-cm diameter) | +8% |
| We assume that large wood litter (>1-cm diameter) is 1.0 Mg C·ha ⁻¹ ·yr ⁻¹ . | |
| Not using additional, larger traps to collect large leaves | -25 to 0% |
| We assume that large palm leaf litter that is not sampled by standard litter traps (cf. Villela and Proctor 1999) can be up to 3.0 Mg C·ha ⁻¹ ·yr ⁻¹ . | |
| Not correcting for leaf herbivory | -7% |
| We assume that 15% of the mass of new foliage is lost to herbivores; we estimate leaf litter (4.4 Mg C·ha ⁻¹ ·yr ⁻¹) as 75% of total estimated fine litter, and we back-calculate the herbivory loss from this value. | |
| Not correcting for precollection consumption of seeds/fruits | -3% |
| We assume that 50% of seeds and fruits are consumed before falling (see <i>Aboveground losses: Aboveground losses to consumers</i>), and that seeds and fruits comprise 5% of the trapped fine litterfall. | |
| Other NPP* components | |
| Not measuring carbohydrates consumption by sap-suckers | -4% |
| We assume that the carbon lost to sap-suckers is 5% of the C in new foliage, which we calculate as leaf litter (0.75 total litter), back-corrected for precollection decomposition (20%) and herbivory (15%) and missed large palm leaves. | |
| Not measuring emissions of biogenic volatile compounds | -8 to -3% |
| We use the estimate of Guenther et al. 1995 for tropical rain forest total BVOCs, and as an upper bound, 3× this value, the (minimum) uncertainty they cite for this value. | |
| Not measuring organics leached from aboveground plant parts | -3% |
| We use the value of leached organics reported for an apple orchard, and assume C is 50% of these compounds (see <i>Aboveground losses: Biogenic volatile organic compounds and leached organics</i>). | |

TABLE 1. Continued.

| Procedure | Potential impact on estimated NPP* (% of NPP* estimate) |
|--|---|
| Not measuring rhizodeposition and C export to nodules or mycorrhizae | -30 to 3% |
| We use the range of values reported in two studies (but the lower estimate, 3%, is for root exudates alone; see <i>Belowground increments and losses</i>). | |
| Assuming coarse root increment is proportional to aboveground increment | -4 to +4% |
| We assume coarse root biomass is 30% aboveground biomass, and calculate potential errors based on the true ratio of coarse root increment to coarse root biomass being from 50% less to 50% more than the ratio of aboveground increment to aboveground biomass. | |
| Not accounting for net increases in fine root biomass | -7 to 0% |
| In aggrading forests, or during recovery from disturbance or climatic stress, fine root mass could increase during the interval. We assume that initial fine root biomass is 1% of aboveground biomass, and that a maximum yearly increase is 50% of initial fine root mass. | |
| Assuming a 1-yr lifespan for fine roots | -25% |
| We assume that fine root life-span is actually four months, and that fine root production was originally estimated (based on annual turnover) at 50% of the 2.0 Mg C·ha ⁻¹ ·yr ⁻¹ of total BNPP originally estimated for the site. | |
| Not correcting for consumption of live roots by soil fauna | -??% |
| There are no data available for estimating root herbivory in forests. | |

Note: Negative values indicate underestimation of NPP* (the percentage by which the original NPP* estimate should be increased); positive values indicate overestimation.

likely to have produced significant underestimates of total forest NPP. This clearly has large implications for regional and global extrapolations of carbon fluxes based on NPP data from field studies.

RELATING FIELD NPP DATA TO WHOLE-FOREST FLUX MEASUREMENTS

Major research efforts are currently being directed at obtaining estimates of forest-level carbon exchange with the atmosphere, using eddy covariance techniques (cf. Goulden et al. 1998, Lindroth et al. 1998, Running et al. 1999, Schulze et al. 1999). These methods are still experimental and incorporate significant uncertainties (Goulden et al. 1996). Concurrent ground measurements at the tower sites can thus be of value for providing cross-checks of the flux data (Greco and Baldocchi 1996).

There are multiple ways NPP* measurements can be used in this context, even though they cannot contribute to a direct quantitative test of tower flux data. The eddy covariance studies measure net ecosystem exchange (NEE) of CO₂ with the atmosphere. The relationship between NPP and this quantity is:

$$NEE = R_h - NPP \quad (1)$$

where NEE is the net flux of CO₂ carbon between the forest and the atmosphere at the site (positive NEE indicates net input of CO₂ carbon to the atmosphere), and R_h is heterotrophic respiration. Thus, NEE is a small difference between two large fluxes. As such, it cannot be validated quantitatively by field measurements. As discussed above, forest NPP* cannot currently be estimated with the needed precision. A change in just one of the many fluxes that contribute to NPP could strongly affect NEE (Frolking et al. 1996). Secondly, it is not currently possible to quantify total het-

erotrophic respiration in a forest with sufficient precision for validating tower-derived NEE.

Nevertheless, there are multiple ways NPP* measurements can be used to provide cross-checks and interpretations of tower flux data. For example, a terrestrial carbon sink indicated by a negative NEE should be manifested as increments in either vegetation biomass, soil organic carbon, or both. If the eddy covariance estimate of NEE exceeds the summed biomass increments (Fig. 1b) for that year, such a disagreement would point either to net accumulation of carbon in the soil, or to problems with one or more of the methods. Rough agreement between the summed increments and measured NEE, on the other hand, would increase confidence in both methods. Similarly, an increase in fine root production and/or fine root stocks from one year to the next would be encouraging support for greater measured nighttime fluxes in the second year. Combining on-going measurements of soil respiration (and, ideally, plant respiration [see Lavigne et al. 1997]) with NPP* studies would further extend the types of comparisons that could be made this way with eddy covariance flux estimates. Given the importance of developing eddy covariance techniques for better understanding ecosystem carbon exchange, it would seem vital at this stage to maintain highly quality-controlled concurrent NPP studies at the flux measurement sites.

CONCLUSIONS AND RECOMMENDATIONS

Existing NPP estimates for the world's forests have been based on incomplete, and in some cases, inappropriate field measurements. As a result, forest NPP may be significantly underestimated. For some forests, it is possible that many of the unmeasured NPP* components are trivial and/or that different procedural errors cancel each other out, with the result that existing

field-based NPP estimates are close to accurate. Determining where and if this is the case, however, will require new field studies that encompass all NPP* components (Fig. 1b), for at least a set of benchmark sites across the major forest types. Although such studies will require intense fieldwork and the resolution of major methods challenges, they should be made a high priority. Without such an effort, great uncertainties will remain with respect to the magnitude of forest NPP, how it varies across forest types, and how it is responding to changing atmospheric composition and climate. To resolve these uncertainties will require both improved practices with current field methods and new techniques for measuring processes such as rhizodeposition and BVOC emission at the forest level. Measurements at each site should be designed to sample in an unbiased fashion across the important gradients of spatial variation, and should be continued through multiple annual cycles. Two critical needs will be documentation of the methods used, and presenting the statistical uncertainty around the estimates of NPP* components. As part of these efforts, the C balance method (Raich and Nadelhoffer 1989) should be extended to provide a first-order estimate of total BNPP at each site; this will require on-going measurement of soil respiration and refined methods for estimating stand-level root respiration (cf. Ryan et al. 1996, Clinton and Vose 1999). Dedicating substantial resources and human effort in a "crash program" of such distributed field studies would greatly improve current understanding of the carbon dynamics of the world's forests.

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