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Estimating Aboveground Net Primary Productivity in Forest-Dominated Ecosystems

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The measurement of net primary productivity (NPP) in forest ecosystems presents a variety of challenges because of the large and complex dimensions of trees and the difficulties of quantifying several components of NPP. As summarized by Clark et al. (2001a), these methodological challenges can be overcome, and more reliable spatial and temporal comparisons can be provided, only if greater conceptual clarity and more standardized approaches to the problem are achieved. The objective of this chapter is to contribute to correction of these limitations in forest NPP measurement. Because Clark et al. (2001a) did an exemplary job with this topic, our task is made somewhat easier. We focus our attention on a variety of practical matters concerning field measurements and calculations for aboveground NPP in broadleaf deciduous, evergreen coniferous, and tropical forest biomes. We evaluate the advantages and disadvantages of contrasting approaches to key measurements and provide recommendations that should aid researchers in designing field campaigns.

In general, field measurement of NPP involves quantifying two distinct sets of organic matter: (1) that which was added and retained by the plants through the measurement interval (net biomass increment) and (2) that which was produced, but lost by the plants during the same interval:

$$\mathrm{NPP} = \Delta \mathrm{B} + \mathrm{M} + \mathrm{H} + \mathrm{L} + \mathrm{V},$$

where ΔB is net biomass increment, and M, H, L, and V are losses owing to mortality, herbivory, leaching, and volatilization, respectively. Clark et al. (2001a) thoroughly reviewed the likely magnitudes and some approaches for H, L, and V, all of which can be significant in certain situations, and we refer readers to that paper for details. Here we focus our attention on approaches to accurate and precise measurement of ΔB (live biomass increment) and M (mortality of living tissues, including litterfall, pruning, stem rot, and tree death). The reason that loss terms such as M must be added to ΔB to calculate NPP can be seen in the case where ΔB is zero: if the live biomass is constant over time, and losses of living organic matter are occurring, then the plants must have replaced this material in the form of new tissue production. These loss terms are therefore equivalent to this new production. Finally, we consider only ANPP in this chapter, since the approaches for belowground NPP are detailed in Tierney and Fahey (chap. 8, this volume). The allocation of carbon (C) to ANPP and BNPP in forests has been the subject of several reviews (Nadelhoffer and Raich 1992; Gower et al. 1996), and remains an important topic for future research because global changes in climate and pollution loading are intimately tied to this balance.

In estimating ANPP as the sum of ΔB and M over some time interval, it is important to maintain consistent and internally complementary definitions of these components. Because of the large size of trees, ΔB is usually estimated by applying allometric biomass equations (developed from carefully harvested trees) to stand survey data, particularly for production of wood and other perennial tissues. Mixed approaches to quantifying M are necessary because of the varied nature of the components of this term. For example, forest ecosystems contain aboveground tissues in the vegetation canopy with both short persistence (less than 1 yr) and long persistence (greater than 1 yr). Tissues with short persistence include deciduous leaves (life span less than 1 yr), flowers, and seeds (from nonserotinous cones). Aboveground tissues with long life spans may include evergreen leaves (life span greater than 1 yr), serotinous cones, branches, bark, and stem wood. The production of short life span tissues is often best estimated with fine litterfall collections (as a component of M), while long life span tissues (especially woody tissues) are best estimated with tree allometric relationships (as a component of ΔB). This is because the former tend to reach a "steady-state" biomass relatively early in stand development. The key point is to avoid double counting or omission of these components in ANPP calculations. Similarly, stand survey and allometric estimates of tree mortality during a measurement interval must be added to ΔB to obtain an accurate estimate of ANPP, but if tissues of dead trees are collected as woody litterfall, then these components of M could be doubled counted. Errors of this sort have been common in the forest NPP literature.

Representative Values and Key Determinants of Forest ANPP

Large projects have been undertaken to summarize and synthesize NPP data to assist in global model evaluation, such as the Global Primary Production Data Initiative described in Scurlock et al. (1999) and Olson et al. (2001). For the present chapter we synthesize a representative suite of these data arranged by forest biome types (table 5.1). There is a tremendous range of aboveground biomass and ANPP for forested biomes. Clark et al. (2001b) have summarized data from 38 tropical forest study sites. We selected 7 sites to include in table 5.1, among them the L'Anguédédou site in the Ivory Coast that had an estimated ANPP of 1430 g C m^{-2} $year^{-1}$. We also in-

Table 5.1. Estimates of forest aboveground biomass and aboveground net primary productivity

	Estimated Aboveground Biomass (g C m^{-2})		Estimated Aboveground Net Primary Productivity (g C m^{-2} year^{-1})		
Forest Type	Minimum	Maximum	Minimum	Maximum	Summary Data Sources
Boreal evergreen	572	8656	120	439	Gower et al. 2001
Boreal deciduous	2644	9334	169	635	Gower et al. 2001
Temperate evergreen	540	49126	60	1555	Grier and Logan 1977; Runyon et al. 1994; Gower et al. 1996
Temperate deciduous	4085	4845	230	555	Gower et al. 1996; Reich et al. 1997; Elliott et al. 2002
Temperate subalpine		12860	36	190	Arthur and Fahey 1992; Hansen et al. 2000
Tropical evergreen	2380	32450	140	1505	Gower et al. 1996; Clark et al. 2001a
Tropical seasonal	15055	22580			Jaramillo et al. 2003
Tropical montane	4696	21850	390	956	Kitayama and Aiba 2002; Jaramillo et al. 2003
Mangrove	1115	35550	305	1350	Sherman et al. 2003
Overall	540	49126	36	1555	This summary

Note: These estimates should be used as a guide for the expected magnitude of ANPP in different forest ecosystems.

cluded data from several studies of temperate forest systems that had ANPP ranging from a low of 105 g C m^{-2} year^{-1} (Ryan and Waring 1992) to a high of 1030 g C m^{-2} year^{-1} (Runyon et al. 1994). Gower et al. (2001) summarized boreal ANPP from 9 sites ranging across North America and Eurasia. The boreal systems exhibited a moderate range of ANPP from 129 g C^{-2} year^{-1} (Gower et al. 1997) to 635 g C m^{-2} year^{-1} (Ruess et al. 1996).

The primary drivers (climatic and biotic) behind the exhibited range in ANPP vary widely. Predominant drivers include soil moisture as influenced by soil water-holding capacity and annual precipitation (Knapp and Smith 2001), N availability (Reich et al. 1997), temperature (Schuur 2003), and light (Runyon et al. 1994). While ANPP generally increases as the magnitude of these drivers increases, in some cases complex interactions can lead to negative relationships; for example, Schuur (2003) noted that NPP declined where mean annual precipitation increased more than approximately 2200 mm year^{-1} because of reduced light. Canopy trees usually comprise the great majority of NPP in closed-canopy forests because they utilize most of the light resource. However, in tropical systems, vine production can be an important contributor and controller of ANPP. Increased vine production as a result of increased atmospheric CO_2 concentrations can cause increased mortality of overstory trees, resulting in a net decline of forest ANPP (Fearnside 1995). As the overstory canopy becomes more open, an increasing proportion of NPP is contributed by understory vegetation. As noted by Vitt (chap. 6, this volume), in boreal forest ecosystems, moss and lichen ground cover is a large contributor to ANPP. O'Connell et al. (2003a) summarized ANPP in black spruce ecosystems with a feather moss understory and a sphagnum understory where 19.7% and 78.2% of ANPP were contributed by the bryophyte and understory layers, respectively.

Guiding Principles and Recommendations for Measuring Forest ANPP

The 3-dimensional structure of forest ecosystems and the perennial age structure of tree woody tissues pose several challenges to accurately measuring forest ANPP. Because the field methods for measuring ΔB and M in forests are typically applied separately to the production of woody tissues, foliage (and other ephemeral tissues), and tree mortality, we organize our detailed review of methods and their limitations in these three categories.

Wood Production

The determination of wood production or woody biomass increment typically involves repeated measurement of tree diameters and the application of allometric equations to estimate changes in biomass from these diameter measurements. We focus our attention in this section on the accurate and precise measurement of tree diameters in fixed-area permanent plots. While variable radius and other "plotless" methods have been used, they are problematical for tree ingrowth, defined as the growth of small trees into the minimum size class used in the forest survey. Neither this size class nor the time interval of remeasurement can be strictly specified, being dependent on the structure and growth rate of the particular forest. Ingrowth will become a significant proportion of the estimated ΔB only when the measurement interval is relatively long (e.g., more than 5 yr). In cases of slower-growing forests, repeated measures are not made annually; rather, the measurements may be made at the start and end of some longer time span and divided by the number of years to determine average annual diameter increment. It is best to make repeated tree diameter measurements during the dormant season, so that the entire annual growth increment can be captured. Consistent measurement season becomes most critical when the measurement interval is short, although it can influence estimates for intervals of up to 10 years by as much as 5%. Tree diameters usually are measured at breast height (1.37 m [4.5 feet] above the soil surface), a common forestry definition (Avery and Burkhart 1983) that avoids swollen tree bases in most, but not all, tree species. For example, special approaches are needed for buttressed trees; Sherman et al. (2003) measured tree diameters above the highest prop root in a tidal mangrove ecosystem to maintain a biologically consistent measurement location on the bases of the tapered stems. On sloping ground it is best to use the uphill side of the tree as the point to determine breast height.

Tree diameters can be measured with a tape that is placed around the circumference of the tree stem. The absolute value of precision for diameter measures is an inverse function of diameter, although as a proportion, precision appears to be relatively constant (fig. 5.1). For example, over a range in DBH from 17 to 125 cm, 2 standard deviations of 7 measurements varied between 0.3% and 1.7% of the mean. The average of 2 standard deviations was 0.8%, indicating that a precision of 1% should be expected for most measurements. Bark sloughing between measurements will result in an underestimate of tree diameter increment or even in a negative growth increment. It may be best to remove any obviously loose bark at breast height before the first diameter measurement is made. Heavy epiphyte growth on stems can also cause errors in diameter measurement; as with loose bark, it may be best to remove these plants before the first measurement and before subsequent measurements. Closely growing trees may eventually grow into each other, causing difficulties in determining individual diameters. One may either measure the combined diameters and partition them according to relative size, or measure the portion of circumference that is exposed. Regardless, it is important to have some sense of relative growth of the trees before they merge. Diameter tapes are easy to use, but care should be taken to make repeated measurements at the same height on the tree stem and at same orientation relative to the axis of the stem. Diameter measurements should be oriented to be perpendicular to the long axis of the stem. This can be ensured by painting or otherwise marking the tree stem at breast height. For many studies, it is necessary to permanently tag trees for repeated census. In this case, the tree tag can be held with an aluminum nail, with plenty of room to grow at breast height, to mark the location of future tree measurements. It is best to avoid using steel or galvanized nails that can corrode over time and cause serious safety issues decades later, when the tree may be cut for future studies or in forest harvesting operations. Galvanized nails can also cause bark necrosis in some species, particularly angiosperms. In plots on very steep ground or in cases where trees are very large, have significant butt swell, or are not growing vertically, it is helpful to have several points marked to assure that diameter measurements are repeatable.

An important issue in the repeated measurement of tree diameters in permanent plots is whether and how to use previous measurements while making current measurements. Often diameter increments will be small relative to the precision of diameter measurements. Checking current diameter measurements against previous values for the same tree will help to reveal obvious inaccurate values (e.g., shrinkage or unrealistic high growth). Cases of unlikely shrinkage would be indicated if the DBH "shrinks" by more than 1%. Cases of unlikely growth would be indicated if the DBH increases more than the expected growth plus 1%. We recommend the following procedure both to reduce measurement error and to avoid possible bias owing to greater circumspection of apparently low rather than apparently high measurements (i.e., it is discomfiting to observe trees shrinking but less so to observe trees growing slightly fast): (1) when first remeasuring a tree, the person with the DBH tape makes the measurement without knowledge of the previous value; (2) the data recorder checks the new value against previous measurements and asks for a remeasurement if there is an obvious discrepancy; (3) if the discrepancy persists, further work may be necessary to resolve the problem.

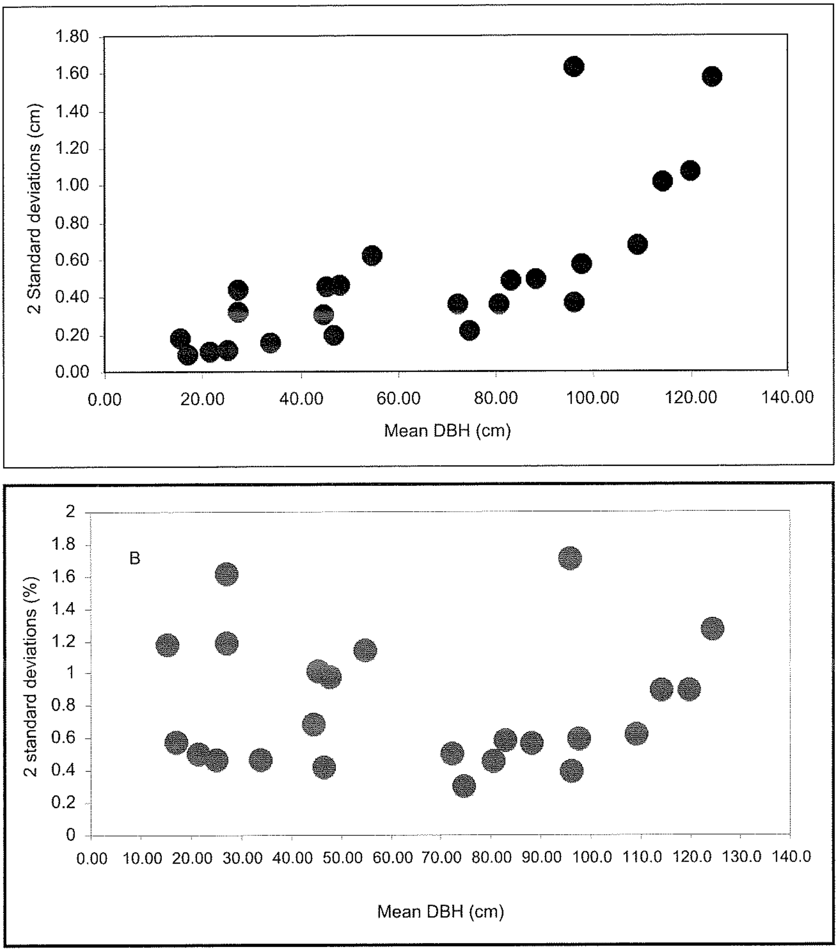

Figure 5.1. Precision of DBH measurements for 24 trees ranging in DBH from 17 to 125 cm. Seven independent sets of measurements were taken. Top panel: absolute difference from the mean expressed as 2 standard deviations as a function of mean diameter. Bottom panel: relative difference expressed as 2 standard deviations as a function of mean diameter.

An alternative to using diameter tapes is to install dendrometer bands on the tree at breast height. These are metal bands that expand as the tree grows. This expansion in circumference can be measured with a digital micrometer, adhesive labels installed with vernier scales, or dial gauges (Heinrich and Banks 2005). The circumference increment can be easily converted to diameter increment. Dendrometer bands provide greater measurement precision than using a diameter tape, but the costs can be high. Dendrometer bands are advantageous when diameter increments are extremely small (for trees growing on extremely cold, infertile, or dry sites), when remeasurements of tree diameter are taken more frequently than once a year, or in forests without distinct growing seasons. They have the disadvantage of expansion and contraction with changes in temperature as well as of detecting moisture- related changes that are not part of the growth signal.

In some studies, a reconstruction of historical tree diameter increment may facilitate the analysis of wood biomass productivity. To accomplish this, the annual growth rings are measured from extracted wood cores. Annual rings are distinguishable in most temperate and boreal tree species; however, many tropical species do not produce tree rings that represent annual growth cycles (Clark et al. 2001a). Therefore, this method is not useful in most tropical ecosystems. The reconstruction of past tree diameter increments facilitates analysis of several years of wood increment during one sampling campaign, rather than having to wait for many years of wood growth after the initial plot establishment. To reconstruct the wood increment, the current tree diameter needs to be measured with a diameter tape. Then a wood core should be extracted from the tree, using an increment borer. One needs to account for the bark as well. As discussed below, most allometric biomass equations are developed for outside bark diameter. Hence, bark thickness should be measured when the core is extracted. Since tree stems are rarely perfectly round in cross section, it is best to extract two wood cores from the tree at a 90° angle to one another. Given the pattern of compression and reaction wood, orienting these cores up and across slope is a good strategy. Because of the often high variation of individual tree growth, at least 50 trees typically need to be measured in each plot sampled. Subsampling in plots with larger numbers of trees is possible with a stratification by size and species. After cores are extracted, they should be mounted in plastic or wood, sanded or trimmed with a sharp blade to clearly expose the annual growth rings, and, if possible, kept moist and cold. Any wood shrinkage due to drying will result in an underestimate of diameter increment of approximately 10%. Alternatively, one can estimate radial shrinkage and make an adjustment to the increments measured. The increments can be measured with an optical dendrometer, dissecting microscope, precision ruler, or scanned and analyzed with a bed scanner and software. After measurement, the 2 growth increments for each year (one from each core) are added to generate the wood diameter increment. Due to internal decay or subsampling, some trees will not be cored. The diameter increment of these trees and the error introduced by this substitution can be estimated using Monte Carlo methods.

The approaches for converting diameter increment measurements into woody biomass production are detailed later in this chapter.

Production of Ephemeral Tissues

Foliage usually comprises a high proportion of the ephemeral tissues produced by trees, although in "mast" years fruits and seeds may be significant in some species (Barnes et al. 1998). Foliage productivity often is easier to estimate than wood productivity, although in cases of young forests with increasing leaf biomass, the same challenges may exist as for wood. The same basic foliage method can be used whether the tree foliage phenology is broadleaf or needleleaf, or the leaf life span is less or greater than 1 yr. Assuming ΔB for foliage is zero, the equivalent of foliage production in forest stands can be measured (as a component of M) with a leaf littertrap. Trees that have a deciduous leaf habit will excise all foliage by the end of the growing season, whereas trees with an evergreen leaf habit contain more than 1 yr of foliage. Evergreen foliage can live for many years; in extreme cases, over 20 yrs of foliage may be retained in the forest canopy (Schoettle and Fahey 1994). In mature evergreen forests the collection of foliage over 1 yr is approximately equivalent to the new foliage produced in the canopy. This approximation is most meaningful over the long term, and at an annual interval is not necessarily related to the actual foliage production for that year.

Numerous approaches have been used for forest litter collection, and the most appropriate approach will depend upon a variety of site-specific factors. In particular, the size and nature of the collection device, the number and spatial arrangement of collectors, and the frequency of collection must be chosen carefully to avoid bias and error. Collectors with a fine-mesh bottom allow drainage of rainwater while retaining most of the smallest litter fragments. Spatial variation in litterfall depends mostly on the canopy structure; for example, higher variation typically occurs for forests of excurrent canopy form (e.g., conifers) than for decurrent form. A sample size of 4 to 6 traps of 0.25 m^2 or larger is usually sufficient to measure litterfall with precision better than ± 5%. The frequency of litter collection must be chosen to minimize losses owing to leaching and litter decomposition; hence, the optimum interval depends upon environmental and biotic conditions affecting these processes as well as the timing of leaf abscission. For example, in the lowland tropics, collecting at 2-wk intervals year-round is often deemed necessary (Clark et al. 2001a), whereas in cold, temperate deciduous forest, collection can be focused on the autumn leaf fall period, with a few additional collections in other seasons.

An alternative to using litter traps for foliage production estimates is to utilize the tree diameter data described above in conjunction with allometric relationships. For deciduous trees, the annual tree foliage production is roughly equal to the estimated foliage biomass from the allometric equation. For evergreen trees, the annual tree foliage production is equal to the estimated foliage biomass from the allometric equation divided by the median leaf longevity in years. If significant amounts of organic matter are resorbed from foliage prior to abscission (Fahey et al. 2005), then this allometric approach will yield systematically higher estimates of foliage production than the litterfall method; the latter may be closer to the actual foliage production, assuming that resorbed organic matter is subsequently utilized in leaf growth. Although the allometric method may not be as reliable as the collection of excised leaf litter, it does provide an estimate of foliage production when other data may not be available. For forests in the early stages of recovery from disturbance, allometric equations can also be used to estimate ΔB of foliage.

Tree Mortality

As mentioned under "Woody Production," depending on the method used to estimate ΔB, neglecting tree mortality will lead to underestimation of woody production. Tree mortality is a crucial component of ANPP calculations that often is not included (Gower et al. 2001). The magnitude of this error will depend mostly upon the time interval between plot censuses. For example, biomass mortality in mature forests typically is in the range of 1%–2% per year; hence, if annual increments from tree cores are used to estimate ΔB, the error from mortality will be small, whereas if repeated measures of diameters of tagged trees at decadal intervals are used, the error will be substantial. Also, in the latter case, the growth of any trees that died during the measurement interval should be added to the mortality estimates described below. Tree mortality estimates can be determined from the same tree census and diameter data collection mentioned in the "Woody Production" section above. Mortality is best determined on trees that have been marked or mapped, as it is extremely difficult to determine the exact year of tree death. It is easy to overlook new mortality unless each tagged or marked tree is individually checked. If mortality data are to be used to determine forest carbon balance, it is helpful to know the proportion of mortality that remains standing versus falling to the ground. Tree mortality is highly variable in time and space. To provide adequate estimates, one needs to sample a suitably sized area over a number of years. Assuming that the death of at least 10–20 trees would form an adequate sample (if all trees were similar in size, this would provide an estimate within 5% to 10% if one tree was added or deleted), a minimum of 5 ha-years (the product of area and time) would be required in many forests.

Understory Production

While understory plants do not comprise a large fraction of forest biomass, sometimes they can form a significant share of the ANPP. For herbaceous, shrub, and moss growth forms, the reader is referred to chapters 3, 4, and 6 in this volume, respectively. For understory trees the methods must be adapted from those for larger trees. Typically a nested subplot can be employed to manage the higher stem density in smaller size classes. Because tagging trees is difficult below about 10 cm DBH and the diameter growth rates of suppressed stems often are very small, estimation of ΔB from resurveys, as described for larger trees, is impractical. Moreover, because these trees normally constitute less than 5% of forest ANPP, the precision of estimates does not need to be as high as for the larger trees. A combination of allometric estimates of understory tree biomass, including carefully measured ring widths on the harvested trees, and periodic remeasurement of densities by size class in nested subplots, normally will provide a sufficient basis for estimating understory tree ANPP.

Allometric Equations for ΔB

General

Diameter increments, obtained either from repeated surveys of individual trees or from wood increment cores, are scaled to woody biomass increments, using allometric equations. These equations are used to relate the easily measured dimension of tree diameter (and sometimes height) to the biomass of various tissues. The difference in biomass between the 2 measurements is divided by the measurement intervals (years) to obtain the annual ΔB.

When possible, site-specific allometric equations should be used because site abiotic and biotic conditions may generate unique tree characteristics that are not captured in general allometric equations from the literature (e.g., Swank and Schreuder 1974; Schreuder and Swank 1974). Nonetheless, many studies involving ANPP will not have the resources or time to develop site-specific allometric equations; in this case, equations developed at sites with similar growth forms can be used, although the degree of similarity is difficult to determine. A survey of the literature may generate useful species-specific or growth-form-specific equations. One informative approach in such cases would be to present the range of estimates obtained from a series of different equations. Currently, the usual approach for studies of lowland tropical forest is to apply the generalized equations of Brown (1997) across all but the most divergent tree growth forms (e.g., ferns, palms). Two extensive summaries of tree allometric coefficients have been compiled that are good first sources for allometric coefficients in boreal and temperate forests. Ter-Mikaelian and Korzukhin (1997) list biomass equations for 65 North American tree species. In addition, they have compiled multiple equations for most species, noting the state or province where the data were collected and the diameter range of the original data, thereby encouraging the user to be cautious regarding the validity of the results when predicting tree biomass. Jenkins et al. (2003) performed a similar review of data in the literature, then produced summaries and used the coefficients to develop general equations rather than to maintain site-specific allometric equations. In this case, their primary objective was to develop national-scale biomass estimators for United States tree species.

The allometric estimates of ΔB are typically developed by harvest of representative trees (see "Recommended Approaches," below). A source of error that is related to, but distinct from, mortality is wood rot and pruning of dead branches in living trees. If the former component is changing significantly in the forest under study, then even site-specific allometric equations that include truly representative trees (as opposed to only healthy ones) will provide biased ANPP estimates. Moreover, because loss of woody material (especially branches) during the sampling interval must be added into the ΔB, ignoring branchfall will result in an underestimate of ANPP (Clark et al. 2001a). Unfortunately, branchfall is highly episodic and spatially variable (Fahey et al. 2005), so that long-term measurements (10+ years) must be obtained on relatively large branch-removal plots (e.g., 25 m^2) to obtain accurate corrections. Also, to avoid double counting, branches from standing dead trees must be excluded from these collections.

Approaches for Developing Allometric Equations

Because site-specific allometric equations are so important, we provide a summary of the method (for additional details, see Whittaker et al. 1974; Martin et al. 1998; or Hanson and Wullschleger 2003). We encourage readers to survey the literature and to refine the methods specific to the wood, bark, branch, and foliar characteristics for the species under study. Typically, at least 10 trees of each species are selected, using a stratified random sampling design (Avery and Burkhart 1983) to ensure that the entire diameter range of trees of each species is sampled. As noted earlier, these trees should be representative of the forest, but because of limitations on sample size and the desirability of obtaining strong regression relationships, some selectivity is needed. Above all, any criteria in sample selection need to be carefully recorded and reported with the equations. Measure the diameter of each tree at breast height (DBH = 1.37 m), fell the tree, and measure the height from the base of the tree to the base of the live crown (BLC), crown length, and total height to the nearest centimeter. For smaller trees mark the live canopy into thirds, remove all branches from each section, and weigh them, using a high-capacity balance. Select a subsample branch from each crown position to determine the ratio of foliage to branch mass. For larger trees, branches may have to be removed while the tree is standing (Brown 1997), and it may be necessary to develop a separate branch mass regression based on branch diameter (and length). To estimate total branch mass, the diameter (and possibly the length) of each branch is measured.

For small trees, cut the stem into sections and weigh each section. Cut a 2-cm-thick disk from the base of each stem section to determine water content. Store tissue subsamples in plastic bags and place them in a cooler (3° C) at the end of the day to minimize moisture loss. For larger trees, it may be necessary to measure the volume of trees and remove disks to determine density. Stem volume can be determined by measuring the diameter at several points along the stem for excurrent forms and at more points for decurrent stem forms. Wood and bark density can be determined from disks by measuring the diameter and thickness to determine disk volume, and weighing the entire disk and taking subsamples to determine the moisture content. Pie-shaped subsamples are ideal because they proportionally weight tissues according to their volume.

For laboratory processing, determine the fresh mass of each subsample and separate the branch subsample into new foliage (present year), old foliage (if multiple age classes are present), new twigs, and wood components. Then dry the tissues to a constant mass at 65°C and weigh them to determine moisture content. In some cases, the drying process may take several weeks.

Calculate the total dry mass of the foliage or branches for a given canopy section by multiplying the ratio of dried foliage or dried branches to the total dry mass of the crown section subsample by the total crown section dry mass. Then sum the total foliage mass and branch mass for the tree across all three canopy positions.

For larger woody parts, weigh the fresh mass of each stem disk and then dry the disk at 65°C to a constant mass and weigh it. For large disks one may need to subsample in order to determine moisture content. Determine stem section dry mass by multiplying (1 – moisture content) by the field wet weight, and calculate total wood mass and bark mass for the section from the ratios of bark or wood to the total disk dry weight. Linear regressions are typically used to compute allometric relationships, using $\log_{10}$ transformed data (to linearize) and the following equation:

$$\log_{10} \mathrm{Y} = a + b^{*}\log_{10} \mathrm{X},$$

where X is the stem diameter in cm at breast height, Y is the dependent variable (e.g., stem wood mass, stem bark mass, foliage mass, etc.), and a and b are the intercept and the slope, respectively. While other forms of equations can be developed by always presenting the recommended equation, a large set of similar equations can be developed rather than a unique form for each study. Another common equation uses diameter and height as independent variables, although when site conditions are very similar, adding height may not explain significantly more variation in the population. In the case of foliage biomass, DBH is not always the best independent variable, especially for larger trees. In this case sapwood area is a better predictor of foliage mass and leaf area; and sapwood area for individual stems can be obtained using increment cores.

The optimal timing for tree harvest varies, depending upon the species and tissue components desired. If foliage mass and/or leaf area relationships are desired, we recommend harvesting trees for developing allometric relationships in the later part of the growing season, after leaf tissues have matured; for evergreen trees the mass of first-year foliage (and twigs) can be obtained, and the median longevity of leaves also should be estimated, if possible.

Special Considerations: Losses to Herbivory, Leaching, and Volatilization

As noted earlier, Clark et al. (2001a) thoroughly reviewed the magnitude and approaches for estimating the losses of ANPP to consumers and via leaching and volatilization of organic matter. Losses to herbivory of leaves and reproductive tissues varies markedly among forest types and between years. In those situations where it is expected to be significant, substantial efforts to obtain accurate estimates are warranted. For foliage herbivory, a combination of measurements of leaf area losses from litter samples and tracking of individual leaves for entire leaf consumption is ideal (Clark et al. 2001a). Predispersal consumption of fruits also may be significant in some forests, but few estimates of this loss are available (Janzen and Vazquez-Yanes 1991; Lugo and Franzi 1993). Finally, losses to volatilization were regarded as a minor proportion of ANPP by Clark et al. (2001a), and Fahey et al. (2005) estimated canopy leaching of organic matter to be 0.9% of NPP in a temperate broadleaf forest.

Plots and Scaling Considerations

The optimal size, number, and placement of sample plots for quantifying forest ANPP vary with the structure and dimensions of the forest and with the aims for scaling the plot measurements to the larger forest. Obviously, larger plots will be needed in lower-density forest composed of large trees than in higher-density stands, but choice of optimal plot size and number may be complex. For example, a few large, individual trees can comprise a high proportion of the biomass in some mature forests, but they could be seriously misrepresented (either over- or under-) in relatively small plots. There will always be some trade-off between plot size and replication. In general, larger plots are more desirable for NPP measurements than those often employed for vegetation composition studies in low-diversity temperate and boreal forests because edge effects are particularly serious sources of error in biomass and NPP estimates.

A general rule of thumb based on the experience of the authors is that the plot size should be chosen to encompass at least 75–100 trees larger than the lower diameter cutoff (often 10 cm DBH). In general, as the plot size increases, the variation between plots decreases (fig. 5.2). Variation should decrease as the number of replicate plots increases, although in some cases the standard deviation can increase as plot number increases (fig. 5.3A). This may be due to the fact that as more plots are added, the actual spatial variation becomes more apparent. If the plot size is adequate, the primary influence of sample size will be on the standard error of the mean, and a large sample size may be required to have standard errors within 5%–10% of the sample mean (fig. 5.3B). The placement of sample plots depends upon the problems and approaches for scaling the plot-based estimates of NPP to the larger forest under study. This consideration can also influence optimal plot size; for example, in complex terrain, if a stratified approach to sample placement is applied (e.g., stratified by slope position), then plot size may be constrained by the scale of terrain units. Researchers should be aware of the likely existence of high spatial variation of NPP within many forested landscapes (Fahey et al. 2005); hence, extrapolation of NPP values from a few plots established on convenient or uniform sites may yield erroneous large-scale estimates. Because the need for relatively large plots often precludes higher replication, the choice of sample placement may be a serious challenge. In sum, because forest structure as well as the approaches for scaling the plot-based measurements will differ markedly among NPP studies, it is not possible to specify uniform recommendations for plot size, number, and sample placement. Nevertheless, these three aspects of the NPP sampling program are critical to its success, and researchers must give them careful consideration and adequate documentation.

Both circular and rectangular plots are commonly employed. The advantage of circular plots is that surveying and marking plot boundaries is not necessary. Rather, by sighting from the plot center with a range finder, any trees near the outer boundary of the plot are checked for possible inclusion in the sample. In hilly terrain it is important to make a slope correction for the sighting distances (or boundary lengths for rectangular plots) because plot areas should reflect projected rather than ground

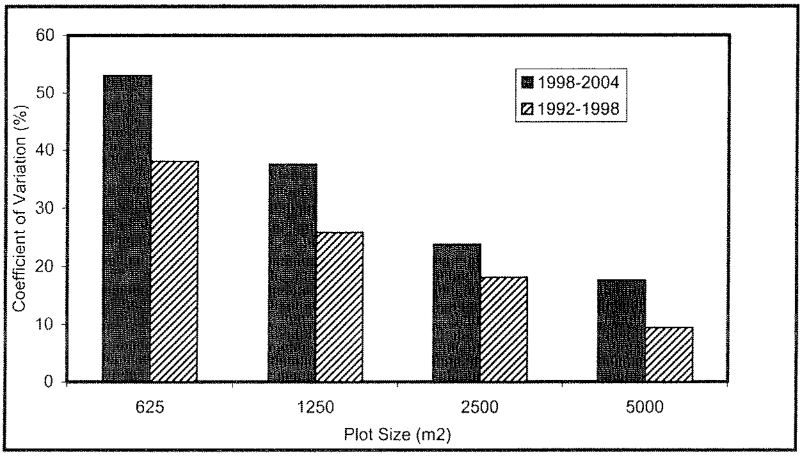

Figure 5.2. Influence of plot size on the coefficient of variation of bole-related NPP estimates on a *Pseudotsuga–Tsuga*-dominated forest in Oregon.

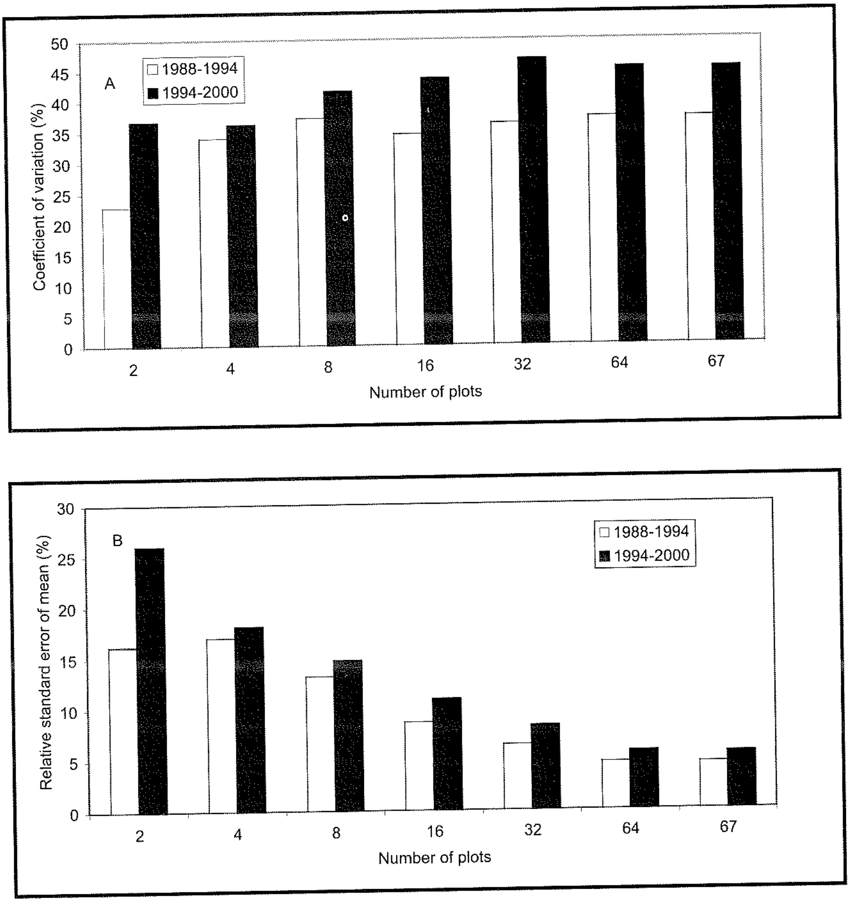

Figure 5.3. Effect of sample size on estimates of the coefficient of variation (A) and the relative standard error of the mean (B) of bole-related NPP. Each 0.1-ha plot was located in a *Pseudotsuga–Tsuga* forest, and the total number of plots was 67. Subsamples of plots were drawn from the data set 20 times to compute the average and standard deviation of NPP.

area. The plot center should be marked with a sturdy stake, and the GPS location recorded. To facilitate relocation of trees and to minimize the chances of "losing" trees, it is helpful to number the trees consecutively in a clockwise fashion.

Future Research Needs

The need for more accurate and precise NPP data from a wider range of forest sites is likely to increase as complex ecosystem models and forest carbon sequestration programs demand high-quality carbon (C) flux estimates for model development and project verification. Both methodological improvements and greater standardization of approaches are needed. As detailed in chapter 12 of this volume, in the future all studies of forest NPP should include explicit consideration of potential biases, sources of error, and quantitative evaluation of uncertainty; these considerations have been sorely missing from most publications reporting forest NPP. Another component that often has been inadequately addressed, but should be part of all standard measurements of forest NPP, is tree mortality (Acker et al. 2002). For this purpose tagged-tree inventories should be a central element of all NPP measurement programs. Finally, the problem of branch litterfall needs to be addressed at all sites. Periodic resurveys of branch-removal plots over several years are needed to improve estimates of this rarely measured component of ANPP.

Most of the other improvements in NPP estimates require that detailed studies, many of which are beyond the capability of routine measurement, be conducted at selected benchmark sites to provide the information needed to correct NPP estimates over a wider range of sites. Based on the analysis of Clark et al. (2001a) and our foregoing discussion, 3 key subjects of detailed, benchmark studies are most critical: (1) losses to herbivory, (2) losses to heart rot, and (3) the allometry of exceptionally large trees. It is clear that in many forest biomes, losses to herbivory are significant, and both temporally and spatially variable. Because of the difficulty of canopy access, remote-sensing approaches to the problem of herbivory losses may be most practical, and interactions between ecosystems scientists and forest pest and pathogen programs are needed. To our knowledge, no estimates are available of the magnitude of bias resulting from not accounting for rot of tree boles. Because most allometric equations are developed using healthy trees, as forests age and an increasing proportion of wood volume is subject to rot, there is the potential for systematic, large-scale overestimation of NPP unless correction factors are applied. Initially, these should be developed for benchmark sites for each of the major forest biomes, in order to evaluate the likely magnitude of error and to direct further efforts.

Finally, and perhaps most importantly, there is an urgent need for the dimensional analysis of very large trees in several forest biomes in order to improve the allometric basis for quantifying ΔB. Trees beyond the diameter range over which allometric equations were developed often comprise a high proportion of forest biomass (Brown and Lugo 1992), and biomass estimates for these out-of-range trees may be highly inaccurate (Brown et al. 1995). Processing of such large trees should be conducted in conjunction with professional forest management operations. Additional measurements of tree form (e.g., diameter at midheight) may also aid in improving the accuracy of allometric estimates of the biomass of such large trees.

In conclusion, forest biomes require additional research, summary, and synthesis on ANPP to better understand annual dynamics in relation to water and nutrient availability and changes in temperature and pollution of the environment. These dynamics will continue to play a major role as global weather patterns change and affect all ecosystems, especially those such as boreal and tropical ecosystems, where marginal changes can have a marked influence on growing season length, water availability, productivity, and C allocation (Gower et al. 2001; Schuur 2003; Beedlow et al. 2004).

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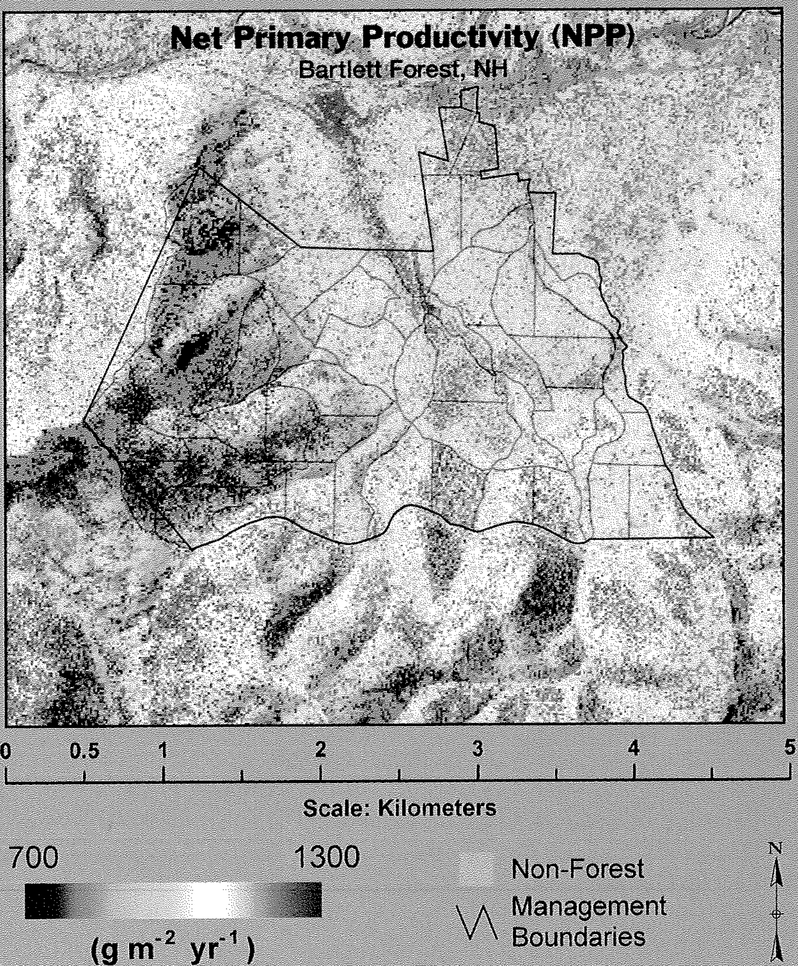

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