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Methods of Estimating Aboveground Net Primary Productivity

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Introduction

Estimating net primary productivity (NPP) has been a central goal of basic and applied ecologists. Very important questions rely on good estimates of NPP: the global carbon balance, the location of the missing carbon sink, and predictions of global climate change (see Chapter 3). Primary productivity represents the major input of carbon and energy into ecosystems and McNaughton (1989) proposed NPP as an integrative variable of the functioning of the whole ecosystem because of its relationships with animal biomass, secondary productivity, and nutrient cycling. From an applied perspective, primary production of grasslands determines forage availability and constrains animal carrying capacity whereas primary production of forests is directly related to wood yield.

The concept of primary productivity is related to the ideas of energy flow in ecosystems (Odum 1971). A portion of the photosynthetically active radiation (PAR, radiation in the 400- to 700-nm wave band) received by an ecosystem is absorbed by green plants (Fig. 2.1). The absorbed energy is either re-radiated, lost as latent heat, or stored by the activity of photosynthesis in organic substances. The last flow is known as *gross primary productivity*. Plants use the stored energy in these organic compounds fixed in photosynthesis for their own respiration (autotrophic respiration). The balance between carbon fixation in photosynthesis and carbon loss in plant respiration is *net primary productivity*, or as Odum (1971) defined it: "net primary productivity is the rate of storage of organic matter in plant tissues in excess of the respiratory utilization by plants." Along the trophic web, herbivores eat part of the organic matter stored in plants (herbivore consumption) but a portion is not consumed and goes directly to decomposers. This flow of matter and energy that represents the fraction of NPP not consumed by heterotrophs is named *net community productivity*. Only a portion of the consumed substances is assimilated since part is lost in animal feces and urine. The assimilated products are then used in supporting heterotrophic respiration or accumulation of herbivore biomass. The rate of accumulation of organic substances in herbivores is named *secondary productivity*. This pattern of partitioning of energy into the categories of assimilated, nonassimilated, and nonutilized is repeated along the food web. Finally, *net ecosystem productivity* is the rate of storage or loss of organic matter in the ecosystem in excess of the respiration by all its organisms in all the different trophic levels from autotrophs to decomposers.

All types of productivity are flow rates of matter and energy through different portions of the ecosystem; they are represented by arrows in the scheme of figure 2.1, and they have units of mass or energy per unit area per unit time (e.g., $g\ m^{-2}\ yr^{-1}$ or $kJ\ m^{-2}\ yr^{-1}$). The terms production and productivity are used as synonyms here. In contrast, biomasses of plants and animals are quantities or state variables where mass and energy accumulate; they are represented by boxes in Figure 2.1, and they have units of mass or energy per unit area (e.g., $g\ m^{-2}$ or $kJ\ m^{-2}$). These two concepts, biomass and productivity, although very different, are often confounded. In part, this confusion arises because biomass is used to estimate productivity in

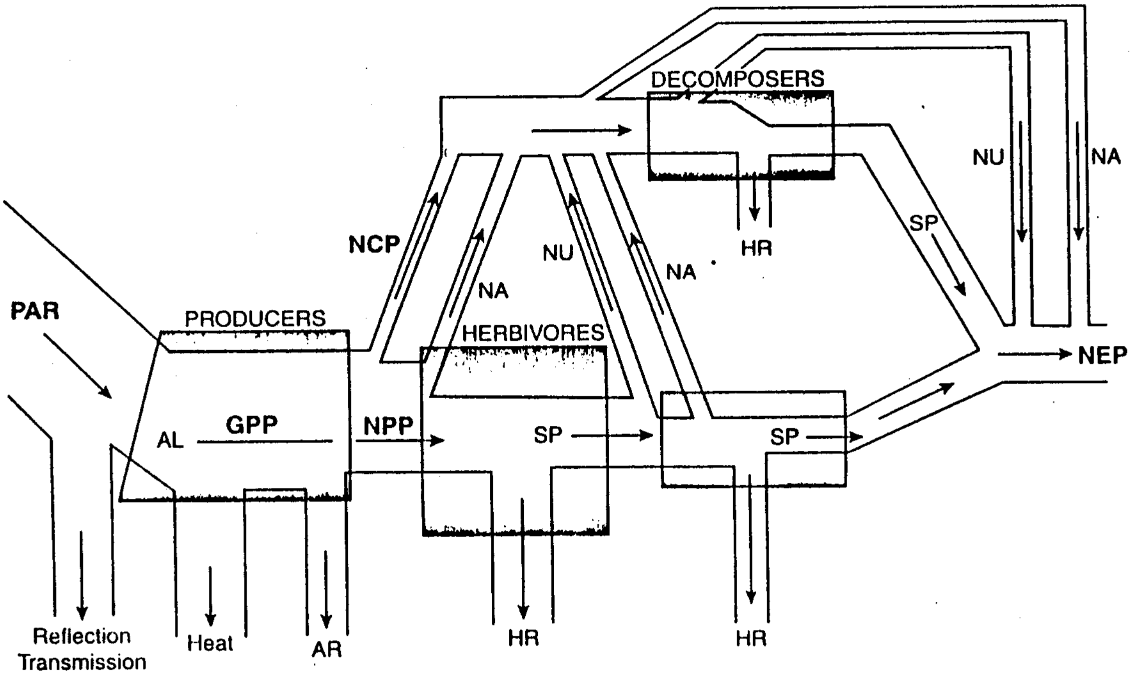

FIGURE 2.1. Schematic energy flow throughout an ecosystem showing the different kinds of productivity. GPP, gross primary production; NPP, net primary productivity; NCP, net community productivity; and NEP, net ecosystem productivity. The associated flows are PAR, photosynthetically active radiation; AL, absorbed light; AR, autotrophic respiration; NU, not utilized; NA, not assimilated; HR, heterotrophic respiration; and SP, secondary productivity.

some cases, as we will discuss later. The concepts associated with both words are identical although production is usually reserved for those cases with an annual time scale. Productivity is usually the preferred term when the scale of interest is less than a year.

The objectives of this chapter are to review the most commonly used methods to estimate aboveground NPP (ANPP) of terrestrial ecosystems using ground measurements and to analyze the tradeoffs among them. This chapter is closely related to several other chapters in this book: Chapter 3 describes remote sensing tools to measure ANPP, Chapter 4 assesses methods for estimating belowground NPP, Chapter 5 reviews the different approaches to measure NPP in aquatic ecosystems, and, finally, Chapter 11 describes micrometeorological techniques to assess primary production. The issue of estimating primary productivity is discussed throughout the book from different perspectives, indicating the importance of the topic and the attention that it has received in ecosystem science.

Different flows and state variables associated with the transfer of energy and matter in ecosystems are measured in assessing primary productivity (Fig. 2.2). *Production* is the flow of carbon from the atmosphere into the *green biomass* of plants. Green leaves and twigs *senesce* and form part of the *standing dead* compartment made up of dead material still attached to the original plant. *Detachment* of dead leaves from original plant incorporates them into the *litter* pool, which is made up of dead plant material lying on the ground. Finally, litter is *decomposed* by the action of microorganisms and part of its carbon returns to the atmosphere as carbon dioxide while another portion is incorporated into microbial biomass or remains in the ecosystem as soil organic matter.

We grouped methods to estimate ANPP in two categories depending on the rate of biomass turnover of the ecosystem. Grasslands and steppes are among the fast turnover ecosystems with high ANPP/biomass ratios, and characterized by small individuals of relatively short life span. In contrast,

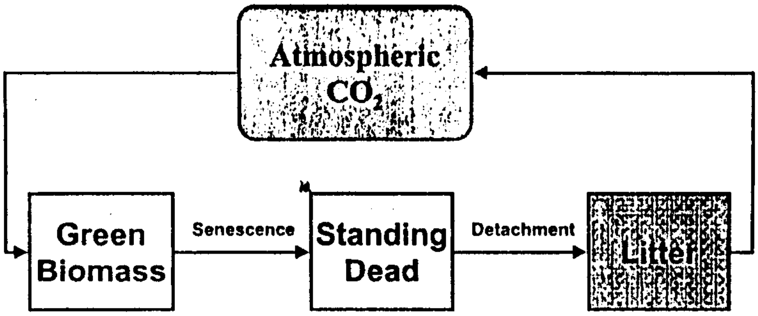

FIGURE 2.2. Schematic of carbon flow through an ecosystem, primary productivity, and the associated flows and state variables used in different methods to assess primary production.

forests belong to the slow turnover rate group with low ANPP/biomass ratio, and large individuals of relatively long life span. Shrubland ecosystems are intermediate between grasslands and forests and usually require the use of a hybrid method combining those of fast and slow turnover ecosystems.

Many methods have been developed to assess primary productivity and many papers have been written on this topic. This chapter describes methods to estimate ANPP in fast and slow turnover ecosystems, and reviews errors and costs associated with the major methods in an attempt to identify costs, benefits, and tradeoffs among the different methodologies.

Methods to Estimate ANPP in Fast Turnover Ecosystems

Singh et al. (1975) thoroughly reviewed the methods for estimating ANPP used during the International Biological Program (IBP) and described the effects of the different methods on the ANPP estimate along the different IBP sites. In ecosystems such as grasslands and steppes, it is difficult to estimate ANPP directly, and most methods take advantage of the characteristics of these ecosystems that live biomass varies broadly among seasons. In some extreme cases, such as the California annual grasslands, green biomass approaches zero during part of the year. In most cases, there are clear minima and maxima for green biomass.

The simplest method to estimate ANPP in grasslands (method 1) is to assess peak biomass and to equate this value with annual productivity. This method assumes that minimum biomass is zero or close to zero and that it increases up to a point (peak biomass) after which senescence starts. It also assumes that there is no carryover from one growing season to the next. Simplicity and low cost are among the most important advantages of this method. A more thorough analysis of the errors associated with this method and the costs and benefits of each method are discussed later in this chapter.

The next method (method 2) relaxes the assumption of no carryover and estimates both minimum and maximum biomass. ANPP is then calculated as the difference between maximum and minimum biomass. This method still assumes a monotonic increase of biomass from a minimum to a maximum value and a separation in time of the processes of production and senescence.

Grassland productivity is usually constrained during the growing season by water availability, which results in a seasonal pattern of biomass with several peaks and troughs (Fig. 2.3). Taking into account just one biomass peak may underestimate total productivity during the studied period. Methods 1 and 2 have the problem of the missing intermediate peaks in biomass since they assume a single maximum. In order to take into account this potential source of error, method 3 relaxes the assumption of the monotonic biomass increase and sums all the differences between consecutive troughs and peaks. This method requires multiple biomass estimates along the growing season instead of one or two as in methods 1 and 2, and therefore significantly increases the costs.

An important assumption of these three methods is that productivity and senescence occur in different periods during the growing season. This assumption may hold only in an annual crop, such as wheat. In most multispecies ecosystems subjected to a variety of stresses, productivity and

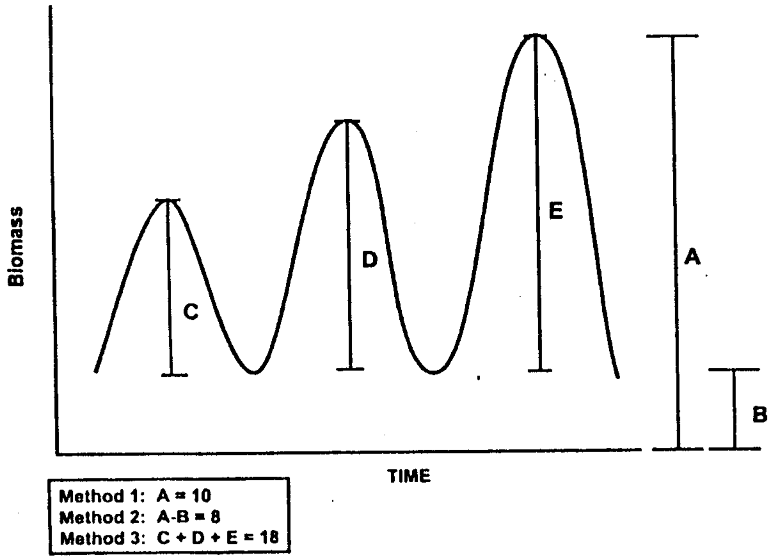

FIGURE 2.3. Idealized seasonal pattern of green biomass. Estimates of primary production using method 1, peak biomass; method 2, maximum minus minimum; and method 3, summation of peaks minus troughs.

senescence occur simultaneously. New leaves emerge at the same time that others senesce or fall to the ground; short periods dominated by production may be followed by others dominated by senescence. The green biomass compartment then reflects the net balance between input and output, productivity and senescence (see Fig. 2.2). Increases in the green biomass compartment underestimate primary production since part of the productivity that occurred during that period replaces tissue that senesced during the same period. It is possible for green biomass to remain constant when production is indeed occurring if senescence is equal to production.

The problem of the simultaneity of production and senescence has been recognized by several authors who suggested different solutions. Wiegert and Evans (1964) proposed to use paired plots, in one of which they harvested dead biomass at time 0 (W0), and in the other they clipped green vegetation at time 0 and harvested dead material at time 1 (W1). Then W1 − W0 yielded the disappearance rate of dead material and this value was added to the estimates of production.

Sala et al. (1981) proposed a method based on a time series of green biomass, standing dead, and litter. The method used data sets in which green biomass was separated among the component species but standing dead and litter were considered in pools undifferentiated by species.

$$\mathrm{ANPP}_t = \sum \mathrm{Pi} + \mathrm{Sc} + \mathrm{Fc} \qquad (2.1)$$

where Pi was the productivity of individual species "I" in the time interval t. Sc and Fc were correction factors that accounted for the simultaneous nature of productivity, senescence, and decomposition.

$$\mathrm{Sc} = (\Delta^{+}\mathrm{SD}/\Delta t) - \sum \mathrm{Si} \qquad (2.2)$$

where Sc represented the increments (Δ^{+}) in standing dead (SD) not accounted for by the sum of decrements in the green biomass of individual plant species (Si). Sc took a value greater than 0 when the sum of all the specific green biomass compartments that decreased during the period was smaller than the increase in the standing dead compartment. Sc assessed part of the productivity that occurred during the period but that it was not detected as an increase in green biomass. Similarly,

$$\mathrm{Fc} = (\Delta^{+}\mathrm{L} - \Delta^{-}\mathrm{SD})/\Delta t \qquad (2.3)$$

where Fc represented the portion of the productivity that was not detected in the green biomass or standing dead compartments. Fc acquired a positive value when the increases in litter (Δ^{+}L) were larger than the decreases in standing dead (Δ^{-}SD).

The errors associated with the simultaneous nature of productivity, senescence, and decomposition probably increase as the diversity of plant species and functional groups of species increases. A single species shows a partial separation in time of productivity and senescence. In contrast, ecosystems made up of species with different phenologies and life cycles, such as early-and late-season species, C_3 and C_4, or annuals and perennials, have a high overlap of productivity, senescence, and decomposition. For example, the senescence of the early-season C_3 species in the Pampas masked the productivity of the late-season C_4-dominated species (Sala et al. 1981). The overlap error becomes less important in ecosystems with lower diversity of species or functional groups. One approach to reduce the overlap error has been to measure productivity by species and then sum them to calculate total productivity.

Estimates of Aboveground Biomass

The discussion about estimates of primary productivity in fast turnover ecosystems assumed that a time series of biomass estimates was available. This section discusses the different ways of obtaining biomass estimates and focuses on how to take into account spatial variability; the temporal variability issue and sampling frequency are discussed in the following section. This section focuses on the issues related exclusively to biomass estimates and does not deal with statistical sampling issues. Sampling is a large section of statistics devoted to the theory and solution of applied problems and its scope goes beyond that of this chapter (Scheaffer et al. 1979).

In grasslands and shrublands, harvests of aboveground biomass have been the most frequently used technique. The number of samples is mostly determined by the variability of the ecosystem and the budget available or the accepted error. The size and shape of the sampling quadrats try to minimize the variance of the estimate (Greig-Smith 1983). The optimal size of the sampling quadrats is related to the pattern of vegetation. The variance of the estimates is maximum when the size of vegetation patches coincides with the quadrat size and decreases as they become larger or smaller. Another consideration is that as the quadrat size becomes smaller, the length of the quadrat boundary per unit area increases. Consequently, the edge effect increases because the person clipping biomass includes individuals or parts of individuals that should not be included and vice versa. Different shapes also affect the magnitude of the edge effect. Circular plots have the lower boundary/area ratio, while rectangular strips located perpendicular to boundaries between patches show lower variance than rectangles and circles. Rectangular strips encompass efficiently the natural variability of vegetation, which otherwise would require huge circles or rectangles. The sampling scheme chosen, which could be random, stratified random, or systematic, depends on the patterns of variability of biomass and on the available budget (see Scheaffer et al. [1979] for a description of sampling techniques' costs and benefits).

After the harvest in the field, biomass is transferred to a freezer as soon as possible to avoid mass losses as a result of plant respiration. Later, material is separated into the different compartments, which can be specific compartments or functional compartments, such as green biomass, standing dead, and litter, depending on the objectives of the study. Finally, the different samples are oven-dried at 70°C for two days to obtain dry weights.

Harvest techniques are expensive and, consequently, many double sampling techniques have been developed to reduce costs. Double sampling techniques consist of establishing the correlation between an expensive variable, such as biomass, and a less-expensive variable, and then using the inexpensive variable in the correlation for future estimates of the expensive variable. Double sampling techniques work as long as the treatment or factor under study does not affect the relationship between the expensive and inexpensive variables. For example, if the purpose of the experiment is to assess the effect of fertilization on productivity and the fertilization alters the relationship between greenness and productivity, then double sampling using greenness is not a good technique.

Capacitance is another variable used for double sampling (Currie et al. 1973; Neal et al. 1976; Neal and Neal 1973; Vickery et al. 1980). Changes in canopy capacitance correlate well with aboveground biomass and small easy-to-use devices have been developed that provide instant readings. Capacitance is mostly correlated with leaf area, and meters need to be calibrated often when water content of the canopy changes. The correlation with dry weight changes with species composition. This is a simple technique mostly used in extension when rapid estimates are needed.

Another group of double sampling techniques uses characteristics of the structure of the community or its individuals. Good results have been obtained using a pin that passes through the vegetation and assesses canopy interception (Frank and McNaughton 1990). The r^2 for the relationship between canopy interception and biomass ranged between 0.831 and 0.956 but the relationship changed with leaf size and thickness, indicating the need to use new calibration curves when there are changes in plant growth forms in space, time, or treatment (e.g., grazed vs. ungrazed plots). At the level of individuals, there are good correlations (r^2 = 0.997) between stem diameter and aboveground biomass for a large number of species spanning orders of magnitude of biomass (Freedman 1983).

Methods to Estimate ANPP in Slow Turnover Ecosystems

Ecosystems with marked differences in the turnover time of their aboveground components represent a challenge for effectively assessing primary production. For example, forests, woodlands, and shrublands have two separate components of aboveground primary production: leaves that are produced in a given time interval, and growth increment of woody material. Each has a different turnover time and the methodology used to estimate its primary production is different. As a result of these characteristics of ecosystems with woody vegetation, proximate measurements of biomass are used more frequently than in the case of systems dominated by herbaceous vegetation.

Production estimates for leaves and small twigs in forests usually involve the use of baskets or litter traps distributed in the forest understory (Whittaker and Marks 1975). The objective is to collect leaves and small twigs over a time course of at least a year, with the litterfall representing the aboveground production in the given time interval. Seasonality of litterfall, rate of litter decomposition, and climatic factors all must be taken into account when designing a sample scheme for litterfall collections. Litter traps should be located at random within a defined plot area, with care taken to avoid edge effects of the plot. The number of litter traps necessary will be determined largely by the heterogeneity of the system, with a minimum of 10 traps per plot area. The traps can be constructed of mesh-screen or nylon fabric, attached to a plastic or wooden frame, and elevated off the ground to avoid contamination with soil and waterlogging. Depending on the dynamics of the forest under study, pickups of litter may need to be completed weekly in the case of some tropical forests (e.g., Wright and Cornejo 1990), at a fixed time interval (e.g., Ogden and Schmidt 1998), or at the end of the season in temperate deciduous forests. Once taken from the field, litter is sorted by type or species and dried in an oven at 70°C for 48 hours for determinations of dry mass.

Additionally, a double sampling technique has been developed to estimate leaf production. Leaf area index (LAI), which is the leaf area in square meters of leaf area per square meter of ground area, is estimated by measuring light intensity at the bottom and top of the canopy using a commercial device called a plant canopy analyzer (e.g., Li-Cor 1992). Leaf area index is then modeled using the following equation: $IL/IO = e^{-kLAI(L)}$, where IL is incident light at the bottom of the canopy, IO is incident light at the top of the canopy, and k is the light extinction coefficient, which varies according to the type of vegetation and angle of inclination of the leaves (Aber and Melillo 1991). Changes in LAI over time can be converted to leaf biomass and used to represent leaf production in forests.

The development of methods for measurements of the woody component of ANPP in forest ecosystems came primarily from yield assessment of lumber for silviculture and forestry. As a result, there is allometric information on many economically important tree species with regression equations that relate tree height and diameter at breast height (DBH) to biomass (e.g., Curtin 1970; Curtis and Reukema 1970). For species that do not have published yield tables, however, which is the case for most nonmanaged forest ecosystems, it is necessary to measure species-specific allometric relationships (i.e., the shape of the trunks and how trunk diameters change with height) in order to estimate biomass and tree production. Because of the logistic difficulty of multiple measurements of all components of woody biomass, dimensional analysis is often used (e.g., Whittaker and Marks 1975; Whittaker and Woodwell 1968). This approach involves taking measurements of several "easy-to-measure" parameters, which, when used with regression equations on a small sample of intensively measured individuals, give information about many of the "hard-to-measure" parameters, including woody biomass and net growth increments. These accessible measurements include DBH, tree height, and basal circumference, which are translated with the use of regression equations to measurements of woody biomass and tree production. In cases in which even the intensive sampling and harvest of even a few individuals cannot be done, some generalizations can be made and they are useful when working in native forests or protected areas where little background information is available. For example, Whittaker and Marks (1975) suggested as an estimate of tree biomass:

$$\mathrm{TB} = 0.5 * \mathrm{BABH} * \mathrm{TH} \qquad (2.4)$$

where TB is tree biomass, BABH is basal area at breast height, and TH is tree height. Similarly, tree production is estimated as:

$$\mathrm{TNPP} = 0.5 * \mathrm{AWI} * \mathrm{TH} \qquad (2.5)$$

where TNPP is tree net primary production and AWI is annual wood increment (at breast height). Additionally, some general relationships of DBH and biomass have been developed for specific regions, such as tropical forests (Brown and Iverson 1992), and in site-specific studies in particular forest ecosystems (e.g., Bormann and Gordon 1984; Raich et al. 1997; Singh et al. 1994).

Wood production per unit area can be estimated in two ways (Binkley et al. 1997). One is to sum the increments of individual trees in a unit area and extrapolate to a hectare basis. Individual increments can be estimated from repeated estimates as described above or using tree cores. The second way of estimating wood production is to make repeated estimates of total stand biomass through time. As will be discussed later, these two different ways of estimating wood production have interesting implications for the estimates of ANPP error.

Branch production is another component of forest ANPP. In some cases, branch plus trunk production can be estimated using regression equations with tree height and diameter (Newbould 1970). When branch production varies among treatments, an independent assessment has been preferred. Researchers have measured the diameter of branches at the base and correlated it with direct measurements of branch dry weight.

Once the woody and branch increments and the litterfall have been accurately assessed, a further complication that can occur in deciduous forests (where some part of the year has substantial light intercepted at the soil surface) is the productivity of understory biomass. In some cases, this vegetation can represent a substantial component of NPP and cannot be ignored or assumed to be a constant fraction of woody production. Peak biomass harvests or sequential harvests over time (such as those described in the previous section) may be used and combined with overstory measurements for the total production estimate.

Shrublands and steppes share characteristics of grasslands and forests and usually require methods that are a hybrid of those used in fast and slow turnover ecosystems. Generally, the two components are assessed separately and combined for a total measure of NPP. Shrubs present some of the same challenges as trees, and various methods have been developed to assess shrub productivity. For example, Fernández et al. (1991) developed a method to measure shrub production in which they harvested annual growth of shrubs (leaves and small twigs) in a small quadrat (10 × 25 cm) located on top of several shrub individuals. They also measured height and two diameters of several individuals. Based on allometric studies of these shrub species and on data about their densities, they extrapolated the quadrat results to a shrub individual and finally expressed their results on an areal basis.

Errors Associated with Estimates of ANPP

The section on estimating ANPP in fast turnover ecosystems highlighted a series of methods to estimate ANPP. The more complicated methods tried to take into account different sources of errors ranging from the missing peaks in biomass to the simultaneous nature of productivity, senescence, and decomposition. All these errors tend to underestimate ANPP. Sala et al. (1988) named this kind of error *errors leading to underestimation (ELUs).*

Singh et al. (1984) and Lauenroth et al. (1986) demonstrated that there are other kinds of errors when estimating NPP that always lead to overestimation of NPP. These are the *errors leading to overestimation (ELOs)*, which stem from the fact that random errors in estimates of biomass do not compensate but accumulate, leading to a positive bias when estimating NPP (Sala et al. 1988). ELOs result directly from the estimation of NPP. In all cases, NPP is estimated as the increase in biomass during a period of time. An increase in biomass during a time period is considered an estimate of production. However, a decrease in biomass in the same interval yields a production equal to zero. Consider the case in which the real value of biomass at time 0 (B0) is equal to biomass at time 1 (B1) (Fig. 2.4). Both B0 and B1 are random variables and therefore, when sampling them, sometimes B1 will be larger than B0, sometimes B0 will be larger than B1, and occasionally they will be equal. Because of the definition of productivity (increments in biomass), when $B1 > B0$ it is considered an estimate of production, but when $B1 < B0$ the estimate of production will be zero. In synthesis, when random errors result in a positive difference, it is accepted as productivity, but when they result in a negative difference, it is ignored.

Singh et al. (1984) and Lauenroth et al. (1986) developed simulation models that yielded "true" values of below- and aboveground biomass and production. They sampled biomass from both models, calculated productivity using several of the standard methods, and compared them against the true values of production from the models. They found that the ELOs were very large; belowground NPP estimates were up to 5 times higher than the true value (Singh et al. 1984) and aboveground estimates were up to 33% higher than the true value (Lauenroth et al. 1986).

The works of Singh et al. (1984) and Lauenroth et al. (1986) were empirical demonstrations of ELOs and their magnitude. Sala et al. (1988) later calculated the distribution function of the estimator of productivity NPP which is nonnormal and demonstrated analytically that NPP derived from changes in biomass is a biased estimator of the true value of productivity. Based on the distribution function of NPP, it was possible to calculate the distribution function of the *overestimation error (OE)* and to assess the determinants of its magnitude.

$$OE = (\sigma/\sqrt{2\pi})e^{-1/2(\mu/\sigma)^2} - q\mu \qquad (2.6)$$

where μ is the true difference in biomass between time 1 and time 0, σ is the standard deviation of the difference, and q is the probability of $B1 - B0 \leq 0$. Independently of the mathematical reasoning that led to the distribution function of OE, it can be

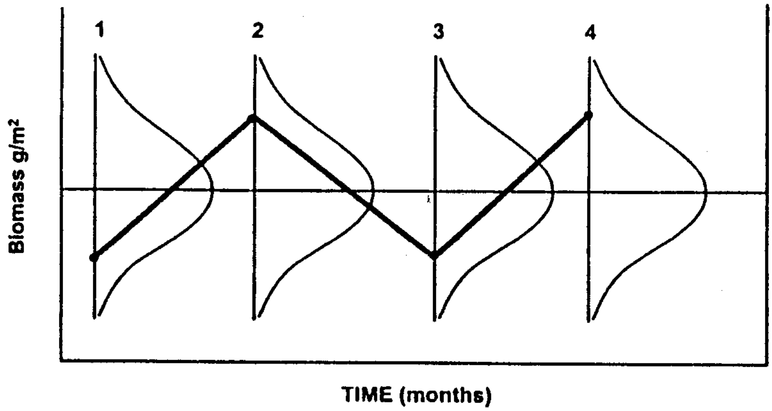

FIGURE 2.4. Example demonstrating how random errors in estimates of biomass do not compensate but rather accumulate and result in a positive bias in estimates in productivity. The horizontal line represents the true value of biomass which, in the example, does not change. Biomass estimates are random variables that have a normal distribution and a mean that coincides with the real mean. Sampling from this normal distribution yields, by chance, values that are slightly higher or lower than the true value. Increases in biomass through time are accepted as productivity but decreases are considered as zero.

seen that the size of the overestimation error depends on the variance and the true value of productivity. The larger the variance and the lower the true value of productivity, the larger is the overestimation error.

The larger the variance of the estimates of biomass used in calculating NPP, the greater will be the possibility of having only by chance a negative difference between biomass at time 0 and time 1 when in fact the true difference was positive. Similarly, the smaller the true value of productivity and of the true difference in biomass (B1 − B0), the higher will be the probability of obtaining by chance only a negative value of B1 − B0. Equation 2.6 indicates that the magnitude of the overestimation error depends on the probability of obtaining by chance a negative value for B1 − B0.

Biondini et al. (1991) developed an example for a grassland with a biomass at time 0 B0 = 110 g m^{-2}, SD = 10, and a biomass at time 1 B1 = 120, SD = 20 g m^{-2} (Fig. 2.5). The distribution of B1 − B0 had a mean of 10 g m^{-2} and a SD of 22.4, and the probability of B1 − B0 being less than 0 was 0.33. The mean and standard deviation of NPP can be calculated using the distribution calculated by Sala et al. (1988). In this example, NPP had a mean of 14.6 g m^{-2}, SD 16.3, the probability of NPP being equal to 0 was 0.33, and the probability of NPP being greater than 0 was 0.67. The overestimation error was 4.6 g m^{-2} and it was cal-

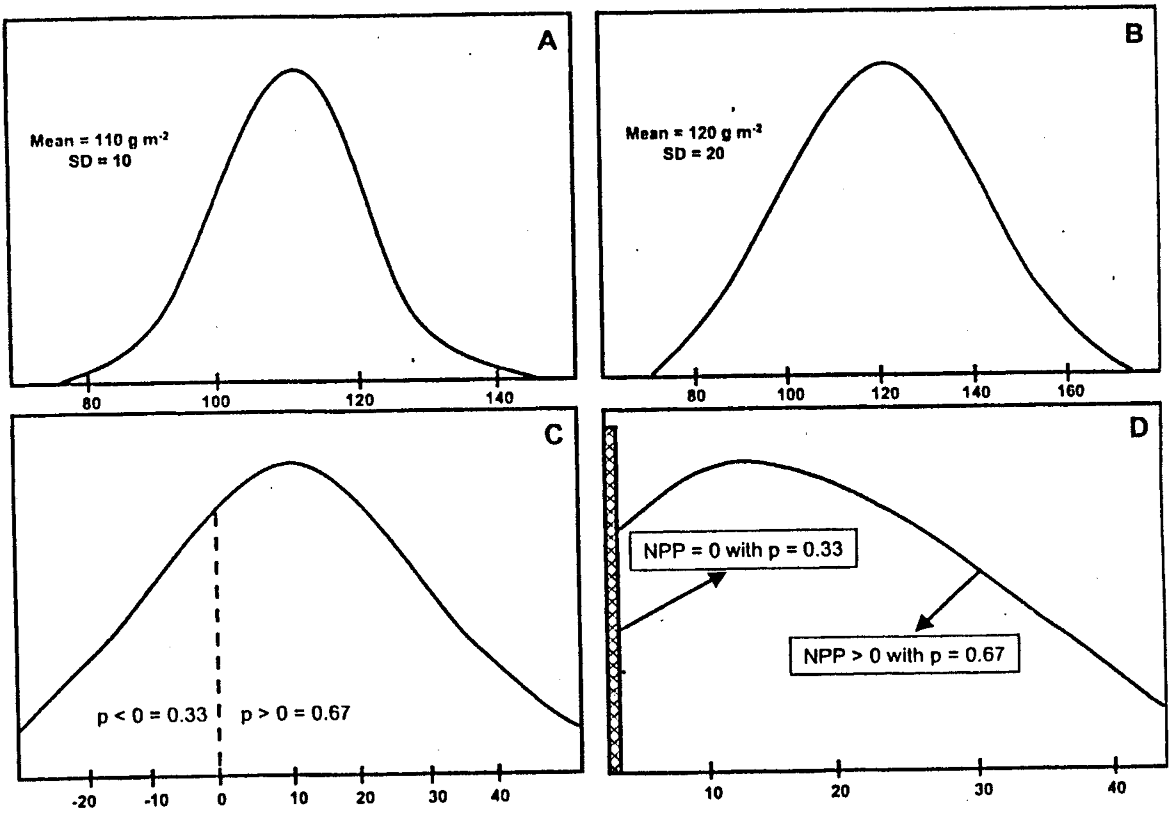

FIGURE 2.5. Example of the occurrence of overestimation error in estimates of productivity. A, Frequency distribution of biomass estimates at time 0. B, Frequency distribution of biomass estimates at time 1. C, Frequency distribution of the B1 − B0. D, Frequency distribution of net primary productivity (NPP) estimates. Note that although the real difference between B1 − B0 is 10 g m^{-2}, in 33% of the cases, the difference B1 − B0 is negative. Because negative values are discarded, NPP estimates are biased and an overestimation error occurs. The mean of B1 − B0 is 10 g m^{-2}, the mean of NPP is 14.6 g m^{-2}, and the overestimation error is 4.6 g m^{-2}. For calculation details see text and Biondini et al. (1991).

culated as the difference between the mean of the distribution of B1 − B0 and the estimated NPP. Biondini et al. (1991) developed software that, given the biomass values at times 0 and 1 and the corresponding standard deviation, calculates OE and corrected NPP value. The software is free and available from M. Biondini, North Dakota State University (biondini@plains.nodak.edu).

Using a similar example, we now show the effect of decreasing the variance of the biomass estimates on the overestimation error (Table 2.1). A 50% reduction in the standard deviation of the biomass estimates with respect to the example depicted in Figure 2.5 (case 1) while maintaining the other variables unchanged, reduces the probability of B1 − B0 < 0 from 0.32 to 0.18 and the overestimation error from 4.6 g m^{-2} (case 1) to 1.1 g m^{-2} (case 2). Similarly, a reduction in the true difference between biomass at time 1 and time 0 increases the overestimation error. In case 3, the variability is the same as in case 1 but the true difference (B1 − B0) is reduced (see Table 2.1). This 50% reduction in the true value of productivity resulted in an increase of the probability of obtaining negative differences in B1 − B0 from 0.32 to 0.41 and a large increase in the overestimation error from 4.6 to 6.5 g m^{-2}.

An important deduction from the analysis of the determinants of the overestimation error is that an increase in the sampling frequency necessarily results in an increase in the error. An increase in the sampling frequency results in a reduction of the true value of productivity that is being estimated. For example, the true value of productivity to be measured when samples are taken monthly will be smaller than if they are taken bimonthly. The reduction in the true value as shown above necessarily results in an increase in the overestimation. The idea just described, that higher frequency results in larger overestimation errors, has been mathematically proven (Sala et al. 1988). Similarly, it has been demonstrated that an increase in error occurs as a result of increasing the number of components used in estimating productivity. For example, estimates of productivity based on the sum of the increases of individual species biomass have a larger overestimation error than estimates based on changes in total biomass.

The errors associated with ANPP in ecosystems dominated by woody plants with slow turnover ecosystems are different from those characteristic of fast turnover ecosystems. Errors associated with litterfall are quite straightforward since the baskets integrate the litterfall flow during a period of time. Consequently, litter accumulated in the traps is an unbiased estimator of true litterfall and there are no errors of under- or overestimation. Sampling errors in estimates of litterfall depend on the forest heterogeneity and the sampling effort, which is mostly constrained by resource availability. Estimates of wood increments have two sources of error, errors estimating average tree growth per tree and errors in extrapolating to a hectare basis. Estimates of tree growth per tree, in turn, have two main sources of error, the estimates of DBH and the error in the allometric equations used to convert DBH data into trunk volume or weight. Tree mortality between two consecutive estimates of stand biomass introduces another source of error when extrapolating from trees to stands (Binkley et al. 1997). The magnitude of this error depends largely on the way stemwood ANPP is calculated. If wood production is calculated by summing the growth per tree in an area, the death of trees during that period represents an underestimation of ANPP. The production of trees that grew during that period and died is missed. Binkley et al. (1997) estimated that tree mortality is usually low and this error would not be larger than 1 to 2% per year. On the contrary, if wood ANPP is calculated as the difference in total stand wood biomass between two sampling dates, the error resulting from tree mortality could be very large. The fall of a big tree will result in a major underestimate of production during the period. All the wood biomass accumulated in the fallen tree during many years is now subtracted

TABLE 2.1. Examples demonstrating the effect of variance and the true value of productivity on the overestimation error of productivity estimates.

	Case	Case 2	Case 3
Biomass at time 0, g m^{-2}	110	110	110
Biomass at time 1, g m^{-2}	120	120	115
B1 − B0	10	10	5
Standard deviation B0	10	5	10
Standard deviation B1	20	10	20
Standard deviation B1 − B0	22	11	22
Probability of B1 − B0 < 0	0.32	0.18	.41
Overestimation error, g m^{-2}	4.6	1.1	6.5

from the estimate of wood production for the study period. Consequently, tree mortality results in a large underestimation error when the method of differences in stand biomass is used to calculate wood production.

Optimal Methodology to Estimate ANPP

The optimal methodology to assess ANPP depends on the objective of the study. Analysis of the errors associated with estimates of productivity provides the tools to choose the best method given certain objectives and budget. Methods that try to minimize ELUs necessarily increase ELOs. The sources of ELUs are the missing peaks and the simultaneous nature of productivity and decomposition. The way to reduce these errors is to increase the sampling frequency to reduce the number of missing peaks and troughs. The increase in the frequency also decreases the possibility of overlap between productivity and decomposition. Estimating productivity by species and then adding them up to assess total NPP also reduces ELUs, as discussed above. However, the increase in sampling frequency and the estimates by species all increase ELOs since they reduce the true value of NPP and increase the variance of the estimates of B1 − B0. Similarly, reductions in the sampling frequency and in the number of components analyzed reduce ELOs but increase ELUs.

If the purpose of the study is to obtain an estimate of annual production, and the ecosystem has a clear seasonality, the best method will be a single harvest at peak biomass. If the ecosystem has even productivity distributed throughout the year or frequent peaks and troughs, a more frequent sampling scheme will be desirable. One possibility of resolving the tradeoff between reducing ELUs and ELOs is to use a detailed method and estimate the overestimation error using the algorithm developed by Sala et al. (1988).

It is important to distinguish between methods that are conceptually more correct and methods that provide an answer that is closer to the true value. Methods that study the independent pattern of individual species or those that take into account numerous functional compartments are closer to the concept of primary production. However, the results that they yield may be further from the real value than those resulting from simpler methods. Here it is crucial to take into account the uncertainty associated with each one of the terms used in the calculation. O'Neill (1973) pointed out that uncertainty of the results increases as the uncertainty of the individual components increases. In the production case, higher variability in the biomass estimates means larger overestimation error. An extreme example is to try to estimate annual production from gas exchange estimates from individual leaves or small patches that then are extrapolated to longer time frames and larger areas. Photosynthesis is a fast variable that varies in a matter of minutes and consequently the errors associated with extrapolating from the leaf to the hectare and from minutes or hours to months and years are so large that they make the results irrelevant. Although the annual estimate of production through the gas exchange method may contain large errors, it may still be very close to the concept of productivity.

Summary

There is not a best method to measure aboveground primary productivity. Decisions about methods are even more complicated, because methods that reduce one kind of error increase other kinds of errors. It is somehow counterintuitive that the more complicated and expensive methods, which take into account most of the flows involved in primary productivity, may yield results with the largest errors. Although these methods are closest to the concept of primary productivity, they may yield results that are the farthest from the real value of productivity. Uncertainty in the variables used to estimate primary productivity results in greater uncertainty in the final estimates of productivity. Because of the way productivity is calculated, uncertainty in the input variables always results in overestimation of productivity. This chapter described of the kinds of errors associated with each method and how they relate to the ecosystem characteristics, as well as the costs and benefits of the different methodological alternatives. The best method will depend on the characteristics of the ecosystem, such as turnover time, seasonality, etc., and on the objectives of the study.

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