

Quantifying Uncertainty in Net Primary Production Measurements

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Net primary production (NPP; e.g., $\text{g m}^{-2} \text{yr}^{-1}$), a key ecosystem attribute, is estimated from a combination of other variables, such as standing crop biomass at several points in time, each of which is subject to errors in measurement. These errors propagate as the variables are mathematically combined, and the distribution of these propagated errors reflects the uncertainty in the NPP estimate. While often not reported, quantification of the component error terms and the resultant NPP estimation error is important for several reasons. First, such information allows the user of the data to assess its reliability. A single-point estimate of NPP does not convey any notion of how good the estimate is, but an estimate with an associated confidence interval does. Second, it allows for more meaningful comparisons because no two estimates will ever be exactly the same. The interpretation of a 10% difference in NPP between two forest stands would be viewed differently if the NPP estimate had an uncertainty of 5% rather than 20%. Third, dissection of estimation error into its constituent components allows one to understand what factors are the major contributors to uncertainty and where efforts might best be focused to reduce this uncertainty.

In this chapter we review concepts related to uncertainty, factors that contribute to uncertainty, and how uncertainty can be estimated, as well as provide examples of uncertainty for selected biomes. While uncertainty is often viewed negatively, we encourage the view that it is just another dimension of understanding an ecological system. Although a major goal of science is to reduce the uncertainty of

prediction, this is difficult to achieve when uncertainty is not quantified or explicitly expressed. Finally, great progress has been made in methods of estimating uncertainty using statistical error propagation and other methods, such as Monte Carlo analysis. Given the availability of software and computers to perform these estimates, this task has become relatively easy.

The Dimensions of Uncertainty

We will use the simple definition of uncertainty as a lack of confidence in a single value, and represent uncertainty about a quantity as a range of potential values in the form of a probability density function (Heath and Smith 2000). The term "error" denotes the deviation of a quantity from its true value. Random errors can vary in direction and magnitude but average out to zero, while systematic errors (or bias) represent a consistent tendency toward deviation in one direction. The distribution of errors is also characterized by a probability density function (e.g., normal distribution defined by a mean and standard deviation or variance) that can be used to represent uncertainty.

Uncertainty can arise from either natural variability or imperfect knowledge (figure 12.1 in this volume; Gardner et al. 1990). Natural variability is inherent in most processes, and includes both spatial and temporal variability. For example, the NPP of 1 m² of grassland varies spatially as one moves across the landscape due to changing microclimate and soils, as well as temporally due to year-to-year changes in weather and other factors. Natural variability cannot be removed as a source of uncertainty through gaining additional knowledge. More intensive sampling, for example, does not reduce the degree of variation among individual members of the sampled population, although it may allow a better characterization of this variation and more precise estimates of the population mean. Knowledge uncertainty includes model error (sometimes called structural error), which results from imperfect representation of processes in a model, and parameter error, which results from imperfect knowledge of the values of parameters associated with these processes. Knowledge uncertainty can be reduced through further measurement or improved models.

Sources of Systematic Error

Bias, or systematic error, deserves special attention because many forms of bias can be avoided or minimized. Bias may be due to errors introduced by (1) the measurement system (e.g., decomposition of litter in traps); (2) improper selection of statistical samples (e.g., only forest areas without disturbance); or (3) the exclusion of certain NPP components. Whenever possible, the accuracy of NPP-related instruments and methods should be checked, and corrections made. The magnitude of bias and any corrections made during the analysis should be reported in the methods description. In theory, improper selection of samples can be dealt with by introducing stratification and randomization, but often estimates are made for subjective "typical" conditions. Abandonment of long-term series of NPP measures

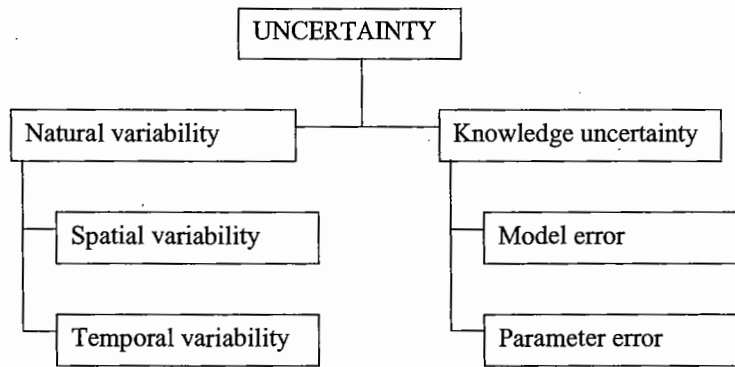


Figure 12.1. Types of uncertainty commonly encountered when making NPP estimates.

from nonrandomly selected sites is often not a practical option. While less than ideal, these estimates can still be useful if the site and conditions are fully described and the measurements can be put in an overall context (e.g., this age class is typically low/high relative to others). The third type of bias is quite common in NPP estimates since certain carbon (C) fluxes are rarely measured, such as C flux to root exudates, mycorrhizae, volatile organic carbons (VOCs), organic leachates, herbivory, and others (Clark et al. 2001). While it is unlikely that all NPP studies can make adequate measurements of all fluxes, values from selected intensive studies can be useful in assigning a likely bias due to omissions.

While having biases is not desirable, the presence of bias does not necessarily make NPP estimates invalid. As with any error, large bias in the estimation of one flux does not mean that the overall estimate is strongly biased. For example, when a small flux is ignored, the overall bias is also small. When estimates are compared over time, bias can be canceled as long as it does not change with time. The same is true for comparisons over space. Bias can be influenced by the time interval between measurements. For example, NPP estimated from increment coring of boles is biased downward because growth of trees that died during the measurement period is not included. For short periods of time (5 yr) this bias is probably <5%; however, for long periods it can become quite sizable, as evidenced by the difference in gross versus net volume growth of forests. For example, by the age of 160 years, the exclusion of mortality in Douglas fir forests led to underestimation of bole-related NPP by 57% (Staebler 1955).

Sources of Random Error

Sampling Error

Sampling error reflects the uncertainty in estimates due to the selection of a statistical sample of units from the population for quantification. For example, if NPP were estimated within 10 randomly selected quadrats in a study area, the mean NPP

would be different if another set of 10 random quadrats had been selected; sampling error quantifies this variability. For mean estimates, sampling error decreases as the number of samples increases:

$$SE_s = \frac{SD_s}{\sqrt{n}} \quad (12.1)$$

where SE_s and SD_s are the sampling standard error and standard deviation, respectively, and n is the sample size.

Measurement Error

Measurement error quantifies the uncertainty in physical measurements that are made in estimating NPP. For example, McRoberts et al. (1994) reported that repeated measurements of the diameter at breast height (DBH) of individual trees in a Michigan forest gave measurement standard deviations of 0.12 cm for 10 cm DBH trees (1.2%), and 0.37 cm for 50 cm DBH trees (0.7%).

Regression Error

Allometric regression equations are often used for nondestructive estimates of plant biomass, especially when the size of the plants makes destructive measurements impractical. For example, a large number of allometric equations have been developed for tree biomass based on measurements of DBH or DBH and height (e.g., Jenkins et al. 2003; Means et al. 1994). While the regression equations represent the best fit lines through the data points for the harvested and weighed trees, the scatter of points about the lines indicates a random error component (figure 12.2; top). Regression standard deviations for predicted biomass, given a value of the independent variable (e.g., DBH), can easily be derived (Dixon and Massey 1983). If logarithmic transformations are used in the allometric equations, a correction factor should be applied to these estimation standard deviations to avoid introducing a systematic bias (Sprugel 1983). As alluded to above, not only random error but also systematic error may be present if the trees to which the allometric equations are being applied are not representative of the population of trees from which the equations were derived. Since regressions from one area are often used for another area, this type of error is quite common in NPP studies. Clearly, variation in growth form due to differences in genetics or competitive status or climatic/edaphic factors might result in either underestimation or overestimation of biomass. Allometric equations should be chosen which were derived under the conditions most similar to which they are being applied (e.g., same geographic region, similar range of diameters, etc.). In some cases there may be more than one allometric equation that can be used, which reflects additional uncertainty in the derived biomass estimates (figure 12.2; bottom).

Conversion Factors

Another potential source of uncertainty in production estimates involves the conversion from one type of unit to another. Conversion factors between different units

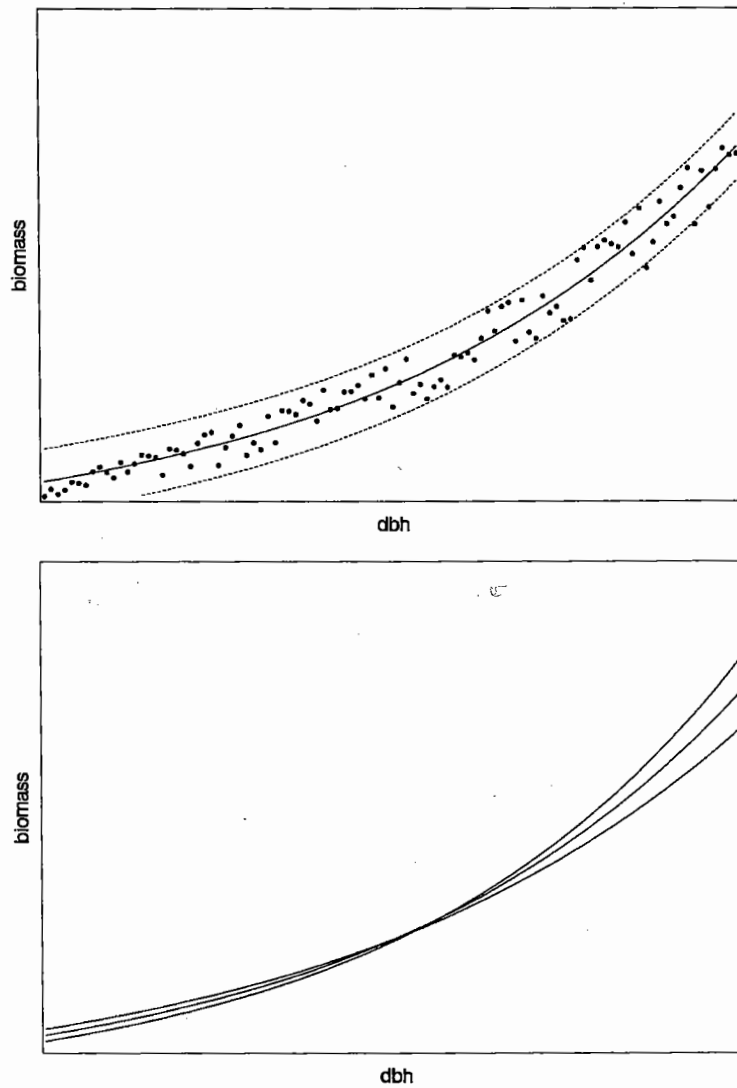


Figure 12.2. (Top): Allometric regression equation for biomass as a function of DBH. Individual data points for equation derivation are shown, along with 95% confidence limits for a biomass estimate given DBH. (Bottom): Multiple allometric equations potentially applicable to a study site. Note that the regression error is highest for larger trees.

that measure the same physical quantity are generally known exactly, and do not add uncertainty to the estimate (e.g., conversion of biomass density from tons acre⁻¹ to g m⁻²). However, conversion from one physical quantity to another may entail additional uncertainty; for example, converting NPP from biomass units (g m⁻² yr⁻¹) to C units such as g C m⁻² yr⁻¹. This conversion is made by multiplying biomass NPP by the proportional C content, which may have some random error due to natural

variability or measurement error. Systematic error is also possible if conversion factors from an inappropriate source are used, such as a different ecosystem, taxon, or growing conditions.

Scaling of Error Terms

Ideally all components of NPP are measured on the same spatial extent or time interval. Practically this is often difficult; for example, tree growth is easy to measure on the scale of hectares, whereas litterfall is not. Likewise, changes in some components can be adequately estimated over days and weeks (e.g., litterfall), whereas others (e.g., tree mortality) may require years to estimate adequately. Therefore, it is necessary to put components on a similar spatial and temporal scale when making an overall estimate of uncertainty. This usually involves aggregating the finer measurements up to the level of the broadest measurements. For example, when combining litterfall (measured on m^2) and tree growth numbers (measured on the scale of $100\text{--}10,000\ m^2$), subsets of litterfall measures should be averaged so that a more reasonable approximation of variation at the larger scale is made (fig. 12.3). This is necessary because it is unlikely that a single small litter trap represents the value at the level of a forest plot. If tree measurements are subdivided spatially, then similar subsets can be used for litter as well. Temporally the process is similar, but may require summation of values within a year and averaging over years. The need to scale error terms does set limits on the spatial and temporal levels for which overall uncertainty can be estimated. Finer-scale measurements (e.g., litterfall measurements at m^2 scale) can be aggregated up to coarser scales to match other

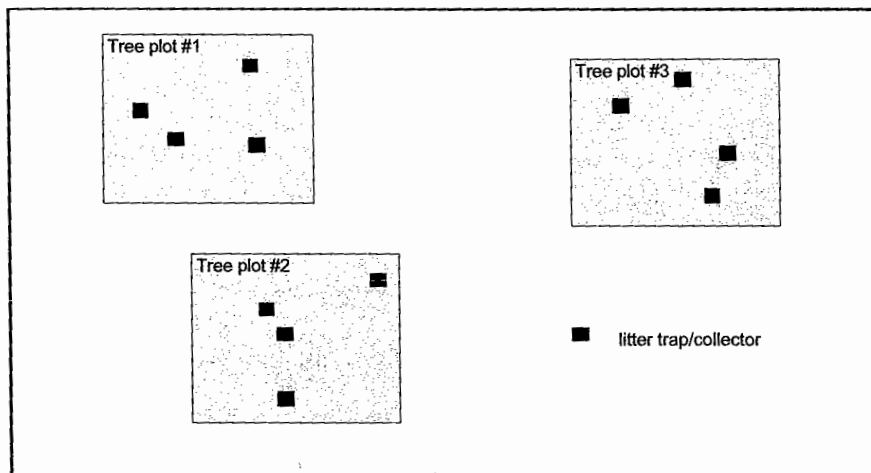


Figure 12.3. Aggregating of samples can be important for calculating uncertainty at the proper scale. Here small litter traps are scattered randomly throughout large tree plots. To combine these terms, an averaging of litter traps within the larger tree plots is desirable.

measurements (e.g., tree growth measurements at ha scale), but the coarser scale measurements cannot be disaggregated down to finer scales because they contain no information on the degree of variability at finer scales. Similarly, on a temporal basis, monthly measurements can be aggregated up to yearly estimates, but not vice versa.

Error Propagation Approaches

Statistical Approach

From a statistical point of view, each of the variables used in a calculation of NPP has some uncertainty, due to the sources of random error discussed above, that can be characterized by a variance. The variance of NPP estimates may be easily determined analytically if they are derived from simple combinations of these variables. In the simplest case, if NPP over a time interval t is calculated as

$$NPP = B_t - B_0 \quad (12.2)$$

where B_t and B_0 are independent estimates of biomass at time t and time 0, then the variance of NPP is equal to the sum of the variances of the biomass estimates:

$$\sigma_{NPP}^2 = \sigma_{B_t}^2 + \sigma_{B_0}^2 \quad (12.3)$$

Other expressions of NPP may involve a greater number of variables, which may or may not be independent (uncorrelated). The variance of a function of several variables can be approximated by a Taylor series expansion (evaluated at the mean of each of the variables) and dropping the higher-order terms (Stuart and Ord 1987). For NPP as a function of multiple variables x_i this leads to the general expression

$$\sigma_{NPP}^2 \approx \sum_i \left[\left(\frac{\partial NPP}{\partial x_i} \right)^2 \sigma_{x_i}^2 \right] + \sum_i \sum_{j \neq i} \frac{\partial NPP}{\partial x_i} \frac{\partial NPP}{\partial x_j} r_{x_i x_j} \sigma_{x_i} \sigma_{x_j} \quad (12.4)$$

where the $\frac{\partial NPP}{\partial x_i}$ terms are partial derivatives and $r_{x_i x_j}$ is the correlation between variables x_i and x_j (Taylor 1997). If the measurements of the variables are independent, and thus have uncorrelated error terms, then the latter term of this equation drops out.

Consider, as an example, estimation of aboveground NPP for a stand of trees according to the equation

$$NPP = (B_t - B_0) + M + L + H + R \quad (12.5)$$

where B_t and B_0 are estimated biomass at time t and time 0, and M , L , H , and R are estimates of mortality, litterfall, herbivory, and removals (harvest) of biomass during that time interval. Assume that estimates of M , L , H , and R and their variances are made by various methods for the entire stand, and that estimates of B_t and B_0 are made by allometric regression on DBH for a statistical sample of individual trees (the same ones each time) and scaled up to a stand-level estimate.

Since the errors in biomass estimation at two times for a given tree are unlikely to be independent of one another (Phillips et al. 2000), we will hypothesize a correlation coefficient of 0.6 for B_t and B_0 (r_{B_t, B_0}). In this example, the partial derivative of NPP with respect to each variable is 1, except for B_0 , which has a derivative of -1; thus, by substituting these values into equation (4), the variance of NPP can be approximated as

$$\sigma_{NPP}^2 \approx \sigma_{B_t}^2 + \sigma_{B_0}^2 + \sigma_M^2 + \sigma_L^2 + \sigma_H^2 + \sigma_R^2 - 1.2 \sigma_{B_t} \sigma_{B_0} \quad (12.6)$$

Note that in this case the positive correlation between B_t and B_0 results in a reduction of the NPP variance compared to the case where they are independent of one another, in which case the last term would be zero. This results from a cancellation of errors. If the biomass for an individual tree were underestimated at time 0 (due to growth form, for example), it is also likely to be underestimated at time t , but these errors may largely cancel one another to give a reasonable estimate of the change in biomass over this period.

As an example of terms combined through multiplication or division, consider converting the NPP estimate derived above to C units instead of biomass units. Thus, equation (12.5) could be written as

$$NPP_c = [(B_t - B_0) + M + L + H + R]C \quad (12.7)$$

where NPP_c is NPP in C units (such as $\text{gC m}^{-2} \text{yr}^{-1}$) and C is the C content of the biomass (g g^{-1}). The variance of NPP_c would be approximated by

$$\sigma_{NPP_c}^2 \approx C^2 [\sigma_{B_t}^2 + \sigma_{B_0}^2 + \sigma_M^2 + \sigma_L^2 + \sigma_H^2 + \sigma_R^2 - 1.2 \sigma_{B_t} \sigma_{B_0}] + [(B_t - B_0) + M + L + H + R]^2 \sigma_C^2 \quad (12.8)$$

where σ_C^2 is the variance of C , the conversion factor for C.

This analytical approach to error propagation can give estimates of the variance of NPP estimates where the equations are tractable and easily differentiated, as may often be the case for computation of NPP. However, there are several other limitations of this method, as was pointed out by Robinson (1989). Error propagation formulas that combine variances for contributing variables, and use variances for calculating specific confidence intervals, are designed for use with normal distributions. If the measured variables have asymmetric, multimodal, or irregular distributions, these formulas are less applicable. Also, first-order Taylor series approximations do not work well when the coefficients of variation (standard deviation/mean) are greater than about 0.3 (Stuart and Ord 1987). Thus, for situations where the equations are mathematically complex, the distributions are irregular, or the coefficients of variation are too high, another method must be used to determine error propagation in NPP estimates.

Monte Carlo Simulation

As noted above, when the complexity of terms or distributions differs widely from normality, another approach is often needed. Monte Carlo simulation can be a useful tool in this context. Monte Carlo simulations utilize information about the uncertainty of components and their distribution to create an overall distribution

(Rubenstein 1981; Fishman 1996). The method is quite simple and involves repeatedly drawing randomly from the component distributions, combining the components, and then accumulating the results (figure 12.4). In addition to saving the individual combinations of results, the mean, standard deviation, or particular confidence levels can be computed.

Monte Carlo simulations can be developed by using many forms of standard statistical programs or by tools developed specifically for this purpose (e.g., Goodman 2003). The key to this analysis is a random number generator to select values of the components, a function that can define the distributions (so that some values of the components are more likely than others), a function that can combine the components, and a function to save the results. The specific software can further process the results, or routine statistical software can be used instead.

Several issues arise before conducting a Monte Carlo simulation, including the size of the error for each component, the distribution of this error, the possibility of co-variation between the error terms, and the purpose of the estimate. If field samples are taken in different locations, this can be used to estimate the sampling error. Measurement errors should be included if they are nontrivial. In some cases, both types of estimates are unavailable; and in this situation, information from other, more detailed studies can be used to set some bounds on the possible error. The range of values observed can be used when a reasonable statistical sample is not available, using the statistical approximation that the range includes ± 2 standard deviations. Multiple types of error distributions can be used, although care must be taken when these are combined (particularly if errors among components are correlated). Commonly used distributions include normal, uniform (all values have equal probability), lognormal, negative exponential, beta, gamma, and triangular (figure 12.5; see McLaughlin 2002 for other possible distributions). The latter distribution is often quite useful because it can approximate many kinds of distributions, yet is easy to parameterize by knowing the minimum, maximum, and modal values. While the exact distribution from which the observed data were drawn is not known, and the use of a best-fit statistical distribution may introduce some unknown degree of error, this trade-off is necessary to provide a quantitative basis for combining sources of variation in the Monte Carlo simulations. Covariance or correlation between components is often not known, but can have an impact on uncertainty estimates (see examples below). In some cases biological theory or understanding of measurements can help determine the degree of correlation. For example, C allocation to one plant part might imply a decreased allocation to another plant part. Or it may be that overinclusion of biomass in one component (e.g., the stem of a tree) might be offset by its exclusion from another component (e.g., the stump of a tree). The final issue to consider is the purpose of the analysis. If, on the one hand, the purpose is to understand the possible uncertainty of individual estimates, then the standard deviations or their analogues should be used. If, on the other hand, the purpose is to understand the possible uncertainty of the estimate of the mean, then the standard errors or their analogues should be used.

In addition to simply combining error components, Monte Carlo simulation can be used to compute the size of individual error components. For example, it can be used for estimating regression error when several allometric equations exist

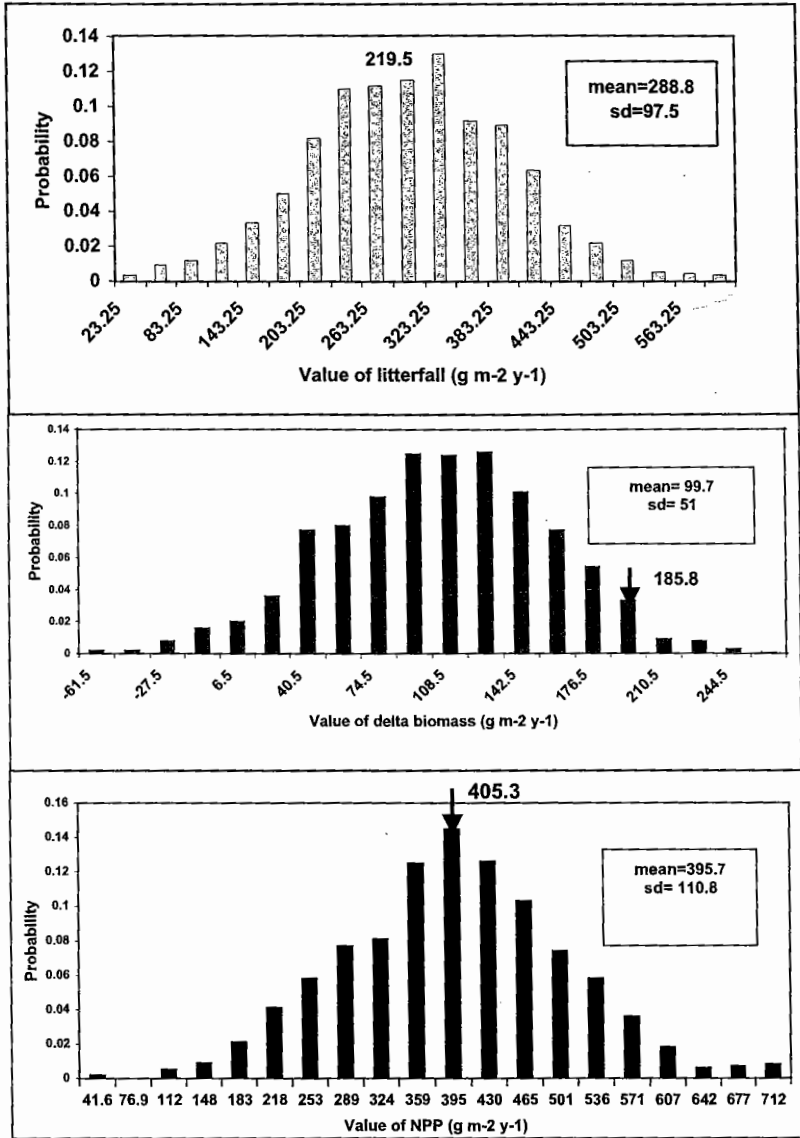


Figure 12.4. Example of component distributions (litterfall and Δ biomass) combined using Monte Carlo simulation to predict a combined distribution using the formula $NPP = \text{litterfall} \pm \Delta\text{biomass}$. A realization value representing one round of calculations is shown with arrows.

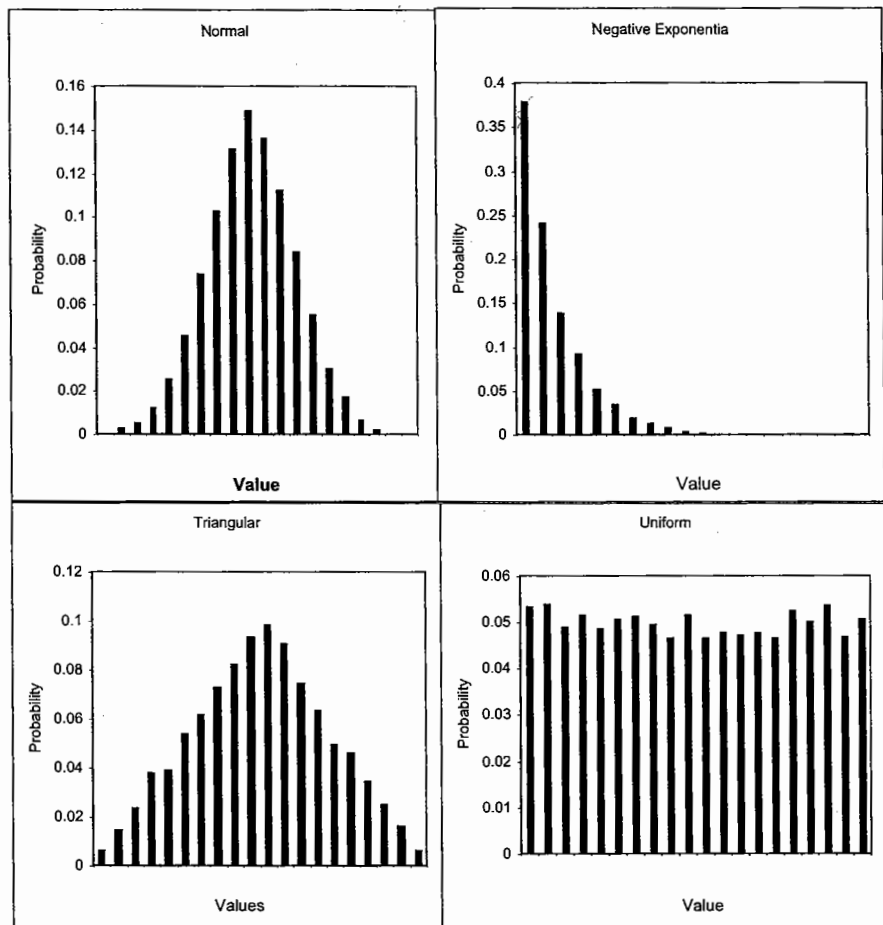


Figure 12.5. Common types of distributions used with uncertainty analysis.

(figure 12.2; bottom). Rather than assuming one equation is correct without comparison against independent data, one could use the range of values predicted by the allometric equations for each size class to limit a random selection of possible solutions. This would be preferable to choosing an equation without any knowledge that it is any better than another possible equation. Another use of Monte Carlo simulation is to estimate growth for plants that were not measured. For example, it is not unusual to use increment cores to estimate growth of trees. While it is ideal that all trees are cored, sometimes the number is too great, and an estimate is determined from a subsample of trees. When trees are subsampled, one needs to apply growth rates from cored trees to those that were not cored. Although one could apply the mean growth increment, this does not provide any estimate of the uncertainty introduced by the subsampling procedure. By using Monte Carlo simulation to repeatedly calculate the possible solutions, such an estimate can be provided.

Compounding of Errors

While there is often an impression that uncertainty expands exponentially as one considers additional sources of error, the degree to which errors compound in NPP calculations depends on the mathematical operations performed, the relative size of the components, and the degree and sign of the correlation among the variables. In general, errors compound more rapidly when variables are combined by multiplication and division, rather than by addition and subtraction. The effect of correlation is dependent on the sign of the correlation and the mathematical operation used (figure 12.6). Positive correlation among variables reduces the compound NPP error when the variables are combined by division or subtraction, because the errors tend to cancel each other, as was illustrated above. Similarly, negative correlation among variables reduces the compound error when they are combined by multiplication or addition. Conversely, positive correlation among variables increases the compound NPP error when they are combined by multiplication or addition, as does negative correlation for division and subtraction.

As far as NPP measurements are specifically concerned, the mathematical operations usually applied involve addition and subtraction of terms, although conversion to C units from organic matter or estimation of belowground NPP from aboveground NPP involves multiplication. A negative correlation between added components therefore typically reduces compound error, whereas positive correlation typically increases compound error. The opposite is true for subtracted components, such as biomass at time t minus biomass at time 0.

Examples of Estimating Uncertainty of NPP in Selected Biomes

This section provides examples of selected biomes in which the uncertainty of NPP estimates has been determined. Our goal is to illustrate real-world examples of errors and their consequences on NPP estimates. Additional analysis of uncertainty regarding NPP estimates can be found in chapter 3 of this volume.

Forest Ecosystems

Though forests contain a range of life-forms, they are dominated by trees that are difficult to measure directly in terms of NPP. An example of the types of measurements taken in forests and their influence on uncertainty of NPP estimates can be found in Harmon et al. (2004). In this study of NPP from a Douglas fir-western hemlock (*Pseudotsuga-Tsuga*)-dominated forest, all trees >5 cm DBH in 12 contiguous, 1-ha plots were measured over a 5-yr period. Mortality of these trees was determined annually. Both changes in tree biomass and mortality were estimated using biomass equations. Litterfall was measured over the course of 3 yr in 4 sets of traps in 4 of the plots, which were averaged to represent a flux at the plot level. Shrub and herb biomass was estimated, and NPP of these life-forms was estimated from leaf longevity and, in the case of shrubs, "rough estimates" of the rate of stem

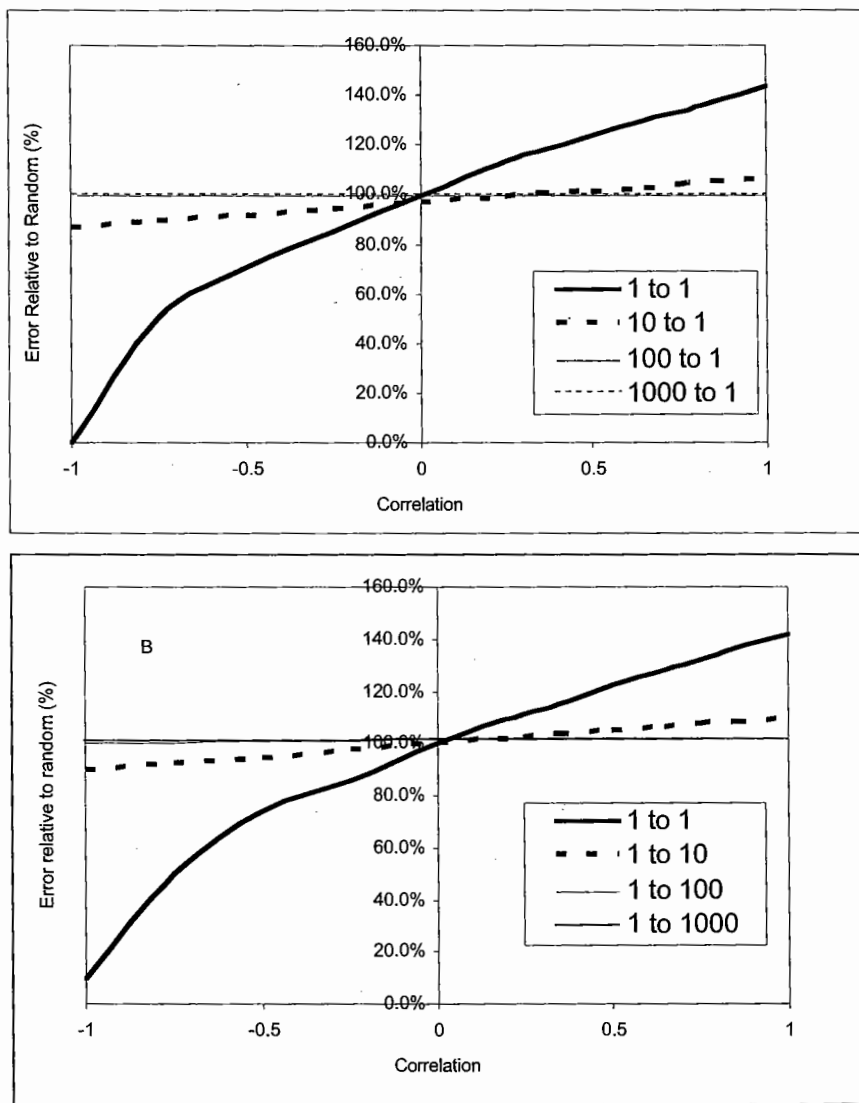


Figure 12.6. Combined error relative to the random error as a function of correlation for different ratios of error between components. The coefficient of variation was set to 10% for both components in the 1:1 case. In the 10:1 case the coefficient of variation was set to 10% for 1 component and 1% for the other, and so on. A = additive terms. B = multiplicative terms.

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mortality. Herbivory was estimated on the basis of the amount of leaf area that had been eaten over a 2-yr period. Belowground NPP was estimated from fine root biomass determined from 20 1-m-deep soil cores and fine root mortality observations derived from minirhizotrons. As with the littertraps, the soil cores were placed in 4 sets in 4 of the plots, and were averaged in each plot to approximate the mean for each plot. For each flux that was measured, the mean and standard error of 1-ha plot-level estimated NPP was computed (table 12.1), and Monte Carlo methods were used to estimate the combined uncertainty, employing random realizations drawn from normal distributions defined by these means and standard errors. This uncertainty was reanalyzed using 10,000 iterations, first by assuming there was no correlation in the fluxes and then assuming there was a positive correlation of 1.0 in all the tree woody tissue-related fluxes. The mean for both estimates was 597.1 $\text{g m}^{-2} \text{year}^{-1}$. As expected, the uncertainty expressed as a standard deviation of estimates for the assumption of positive correlation of tree woody tissues was higher ($47.7 \text{ g m}^{-2} \text{year}^{-1}$) than for assumption of no correlation of fluxes ($44.8 \text{ g m}^{-2} \text{year}^{-1}$). However, expressed as a ratio of the mean, both assumptions gave an uncertainty of NPP of $\sim 8\%$, which implies that 95% of the estimates were within $\pm 16\%$ of the mean estimate.

Table 12.1. Estimated stores of carbon and rates of production associated with live biomass in a Douglas fir/western hemlock forest

Pool	Store g C m^{-2}	Δ Store $\text{g C m}^{-2} \text{y}^{-1}$	Mortality/litterfall $\text{g C m}^{-2} \text{y}^{-1}$	NPP $\text{g C m}^{-2} \text{y}^{-1}$
Stem sapwood	6567 (198)	2 (1)	30 (9)	32 (9)
Stem heartwood	15,351 (1151)	26 (2)	50 (13)	76 (13) ^d
Stem bark	3337 (263)	2 (4)	12 (2)	14 (3)
Live branches	4489 (112)	8 (10)	100 (34)	108 (34)
Dead branches	318 (20)	0 (0) ^a	3 (1)	3 (1)
Tree foliage	941 (322)	0 (0) ^a	135 (12)	150 (14) ^e
Coarse roots	8122 (639)	21 (7)	30 (5)	51 (7)
Fine roots	362 (26)	0 (0) ^a	91 (16) ^f	91 (16)
Understory shrubs	144 (37)	0 (0) ^a	26 (5) ^b	26 (5)
Understory herbs	76 (8)	0 (0) ^a	40 (8) ^c	40 (8)
Epiphytes	100 (25)	0 (0) ^a	6 (1)	6 (1)
Total random	39,807 (2479)	59 (24)	523 (69)	597 (44.8)
Total positive corr.				597 (47.7)

^a The net change in stores in these pools was assumed to be zero.

^b It was assumed that all leaves from shrubs died each year and that 0.5% to 1% of the stems died. Litter traps indicate that the value of shrub litterfall may be as low as $1 \text{ g C m}^{-2} \text{y}^{-1}$.

^c It was assumed that litterfall from herbs was 40%–60% of live stores to account for the fact that some small, woody, stemmed, evergreen plants are included in the herb category.

^d It was assumed that no heart rot is present.

^e This includes grazing of $15 \text{ g C m}^{-2} \text{y}^{-1}$.

^f It was assumed that 20% to 30% of fine roots die annually.

Note: Mean (standard error).

Source: After Harmon et al. (2004).

Savanna Ecosystems

The co-dominance of tree and grass life-forms in savanna ecosystems (House et al. 2003) produces high spatial variability in NPP. Monte Carlo methods were used to quantify the sources of uncertainty of the major aboveground components (live wood, herbaceous plants, and litter) of NPP in blue oak (*Quercus douglasi*) savanna in California (Battles et al. in press). The primary sample unit for this analysis is the plot, in which tree diameters, litterfall, and herbaceous plant growth were measured. Dendrometer bands were installed on a size-stratified subsample of trees within these plots to estimate stem diameter increment. Several plots were established in a stratified random manner (strata based on canopy cover class) to characterize the larger study area, and nested subplots were located within them for litterfall and herbaceous vegetation measurements. The following sources of error (table 12.2) apply to the plot-level estimates: (1) regression errors in the equations predicting mass parameters from tree diameter; (2) model errors in the application of the tree growth model; and (3) sampling errors for the components subsampled within plots (herb and litterfall). Allometric equations for oak tree biomass were developed on-site; published equations were used for pine (Jenkins et al. 2003), which accounted for only 20% of the basal area. Measurement errors for tree diameter and weighed biomass are regarded as minor, and were not included.

A Monte Carlo analysis with 1000 randomizations of the subplot-level data was used to estimate means and standard deviations for each pool and flux. Errors were assumed to be normally distributed, and standard errors (or their equivalents) were used to propagate uncertainty. Biomass pools and fluxes for the strata were based on 1000 randomizations of the plot-level data (i.e., results from subplot-level randomizations), assuming a normal distribution characterized by the mean and variance of each pool or flux. The 2.5 and 97.5 percentiles were used to determine the confidence intervals (95%) of study area means. Of the components of NPP considered here (table 12.2), leaf litterfall had the greatest within-plot variation with a mean coefficient of variation (CV) equal to 34%. The herb component was the next most variable, with a CV equal to 19%. Most of the variation in wood production was due to uncertainty in the growth model (CV = 14%). In comparison, allometric regression model imprecision was 6% CV. Together, the growth and allometric regression models produced plot-level estimates of aboveground wood production with a CV = 15%. In any uncertainty analysis it is instructive to note the sources of these errors. For both litterfall and herbs, plot-level variation stemmed from the high spatial heterogeneity within the plots. For the trees, uncertainty resulted from the growth projections and allometric equations. Propagating these errors to the watershed scale, by area-weighting the results from the four strata, resulted in a 95% confidence interval equivalent to $\pm 18.9\%$ of the mean estimate. For comparison, the watershed estimate of NPP was calculated assuming that plot-level uncertainty was zero. The results were a mean with a small positive bias (+4%) along with the expected smaller estimate of uncertainty (table 12.2).

Table 12.2. Sources of uncertainty in NPP estimates: Small watershed, blue oak savanna of California

Component	Source of Error	Plot-Level CV (%)	Plot ID	NPP Plots (g m ⁻² ha ⁻¹)		Strata (% tree cover)	NPP Strata (g m ⁻² ha ⁻¹)		NPP Watershed (g m ⁻² ha ⁻¹)	
				Mean	SE		Mean	SE	Mean	SE
Live Wood	Sampling	—	215	252	52.5	>60	371	35.1	306-441	
	Regression Model	6	216	374	40.0	>60	399	32.0	(387) (29.1) (330-444)	
	Total	15	221	573	72.5	>60				
				204	242	38.2	30-60			
Litter	Sampling	34	206	293	49.3	30-60	291	32.3		
	Regression Model	—	207	337	76.8	30-60				
	Total	34	203	256	33.1	15-30	364	27.2		
			211	473	56.0	15-30				
Herb	Sampling	19	213	361	57.5	15-30				
	Regression Model	—	202	705	213.9	<15	442	74.0		
	Total	19	220	278	49.6	<15				
				208	336	17.2	<15			

Notes: SE = standard error of the mean; CV = coefficient of variation; 95% CI refers to the 95% confidence interval of the mean. Values in parentheses under "NPP watershed" are estimates without plot-level error.

Grassland Ecosystems

While determining peak biomass of grasslands is a relatively simple, direct measure of ANPP, many have argued that other terms, such as losses to mortality, grazing, leaching, volatilization, and decomposition of recently senesced plants, should be considered to reduce bias (chap. 3 in this volume). An analysis conducted by Lauenroth et al. (in press) examined how bias and uncertainty changed with addition of terms, using data collected from the Chapingo site grassland, which is located approximately 20 km northeast of Mexico City (19° 27' 30" N, 98° 54' 30" W) at 2241 m elevation (Garcia-Moya and Castro 1992). Mean annual precipitation is 579 mm, and mean annual temperature is 15.1 °C at this site. An interesting feature of the study by Garcia-Moya and Castro is that many NPP-related terms were quantified with different methods. This allowed Lauenroth et al. (in press) to use Monte Carlo simulations to assess the relative variability in NPP estimates obtained using six different NPP estimation equations that varied in both the number of parameters and the intricacy of mathematical operations (table 12.3). Lognormal distributions were generated using the mean and standard deviation of each input variable to generate input for a total of 20,000 random estimates for each method. Because many of the means were associated with large standard deviations, the lognormal distribution was used to guarantee that all of the random values were equal to or greater than zero. The results indicated that more complex equations may result in greater uncertainty without reducing the probability of underestimation bias. For example, harvesting the peak live and dead biomass one time (method 2) resulted in a CV of 22% to 27%, whereas summing all the positive increments of live and dead multiple times over the year (method 5) resulted in a CV of 94% to 86% for the 2-yr period considered (table 12.3). The mean NPP estimates for methods 2 and 5 were 1287 and 801 g m⁻² yr⁻¹ and 1031 and 743 g m⁻² yr⁻¹, respectively for the 2 yrs considered. Thus, while it could be argued that some methods, such as peak live biomass, underestimate ANPP (the mean ANPP for this method was the among the lowest: 316 to 254 g m⁻² yr⁻¹), the inclusion of dead biomass in the annual harvest eliminates this bias without increasing uncertainty as much as more complex and time-consuming methods. As could be expected from our general review above, the amount of uncertainty associated with estimates of NPP was influenced by the number of parameters as well as the variability in the data and the nature of the mathematical operations. By standardizing input data to "control" the variability in the data, Lauenroth et al. (in press) were able to demonstrate that equations with product terms (such as the inclusion of decomposition losses) have the potential to magnify the uncertainty in the estimates of NPP. This analysis suggests that more complex NPP estimation equations can increase uncertainty without necessarily reducing risk of underestimation.

Kelp Forest Ecosystems

Marine forests of the giant kelp *Macrocystis pyrifera* are widely distributed in cool seas of the northern and southern hemispheres (Wormersley 1954) and are among the most productive ecosystems in the world (Mann 1973, 2000). The wave-swept

Table 12.3. Means ($\text{g m}^{-2} \text{yr}^{-1}$), standard deviations ($\text{g m}^{-2} \text{yr}^{-1}$), and coefficients of variation (%) for aboveground net primary production

	Peak Live Biomass ^a	Peak Standing Crop ^b	Max-Min Live Biomass ^c	Sum of Positive Increments Live Biomass ^d	Sum of Positive Increments Standing Crop+Litter ^e	Sum of Changes Live and Dead, Adjusted for Decomposition ^f
<i>1985</i>						
Mean	316	1287	265	164	1031	864
Std Dev	54	283	56	251	965	371
CV	17	22	21	153	94	43
<i>1987</i>						
Mean	254	801	239	241	743	661
Std Dev	110	213	110	101	638	254
CV	43	27	46	42	86	38

^aNPP estimated from peak live biomass.

^bNPP estimated from peak standing crop of live plus dead, assuming biomass produced during the interval of interest senesced before sampling.

^cNPP estimated from the difference between the minimum and maximum estimates of live biomass, assuming some live material is carried over from the previous intervals.

^dNPP estimated by summing all of the positive increments in live biomass, assuming that live material is carried over from the previous interval and that there are multiple peaks in live biomass.

^eNPP estimated by summing of positive increments in live biomass, standing dead biomass, and litter. An increment in live biomass also corresponds to an increment in total dead (standing dead+litter) with same assumptions as method 4.

^fNPP estimated by summing the changes in live and dead biomass (positive or negative) and the amount of material that decomposed during the interval.

Source: The data are from a grassland in Chapingo, Mexico, and are based on data from Garcia-Moya and Castro

habitat in which giant kelp lives, coupled with its large and complex morphology, rapid growth, and high turnover, introduces many sources of uncertainty when attempting to estimate NPP. Researchers at the Santa Barbara Coastal LTER have been estimating NPP of giant kelp at three sites in southern California since 2002 (Reed, Rassweiler, and Arkema unpubl. data). Monthly estimates of NPP are obtained by measuring biomass changes in fixed plots and accounting for losses of whole plants as well as fronds of surviving plants (each plant consists of many fronds arising from a single basal holdfast). Biomass is estimated from diver measurements of the density of plants and their morphology, which are then converted to dry weight based on empirically derived relationships between morphometric data, such as plant length, and wet weight. Losses are estimated from changes in plant density in the fixed plots and from losses of fronds on a subset of tagged plants. Sources of error include observer error in estimates of biomass and plant loss, sampling error in estimates of frond loss, and regression and model error in the conversion of morphometric data to dry weight (table 12.4). Because errors in estimates of plant density and biomass within a plot are correlated, the error in biomass is treated as a function of the error in density.

Table 12.4. Sources of uncertainty in NPP estimates for a kelp forest in southern California

Component of NPP	Type of Error	Error Distribution	Scale Applied
Biomass	Observer	Normal (CV: 15 %)	Plot
	Sampling	—	
	Model	Normal (CV: 21%)	Plant
	Regression	Bimodal	
Plant loss	Observer	Normal (CV: 15%)	Plot
	Sampling	—	
	Model	—	—
	Regression	—	
FronD loss	Observer	—	—
	Sampling	Normal (CV: 12% to 30%, depending on number of plants sampled)	
	Model	—	—
	Regression	—	

CV = coefficient of variation.

Monte Carlo simulations were used to quantify uncertainty in this system because one of the errors is not normally distributed and because the calculations of annual kelp NPP use particular measurements multiple times. Four of the five sources of error used here can be approximated with a normal distribution, but one cannot: the distribution of length:weight conversions has a bimodal shape. Monte Carlo methods also easily incorporate situations in which particular errors enter into a calculation multiple times. For instance, an observer who overestimates the biomass at a given time will cause an overestimate of NPP for the previous month, because the change in biomass will appear more positive, but an underestimate of biomass in the following month, when the change in biomass will appear more negative. The negative correlation between errors in adjacent months does not affect the uncertainty in NPP for a particular month, but when production is calculated on an annual scale, these monthly errors tend to cancel out, and the total uncertainty is reduced. In the calculations of kelp NPP, the median standard error for monthly estimates of production is ~30% of the production, whereas the standard errors for the annual estimates are less than 10% of the annual production.

Aquatic Ecosystems

Uncertainty estimation of NPP in aquatic ecosystems with microalgae as the dominant producers involves errors from methods that are very different from those used

in the above ecosystems. In fact, due to the inability to separate autotrophic from heterotrophic respiration, NPP is difficult to estimate using O_2 flux measurements; therefore, production estimates in aquatic systems consider GPP rather than NPP. Chamber estimates of aquatic ecosystem metabolism and GPP contain both measurement uncertainty and considerable spatial uncertainty when scaled up. Additionally, chambers may not represent the entire ecosystem, which may introduce bias. For example, respiration estimates from surface chambers do not include the hyporheic zone, resulting in underestimation of total stream respiration (Fellows et al. 2001). The number of chambers necessary to characterize metabolism in a particular ecosystem depends upon the spatial heterogeneity relative to the size of the chambers; thus investigators should estimate variability from preliminary data to determine the number of replicate chambers necessary for their particular question.

Within a reach of a river or lake, free-water or open channel estimates of metabolism do not suffer from spatial scaling error as chambers do. However, measurements from one reach of a river or from a lake may not be representative of other reaches or lakes, and temporal variability is often high, so measurement at one time may not represent other times (Uehlinger and Naegeli 1998). Open channel estimates can involve bias such as that caused by groundwater movement into a river. The groundwater usually has a much lower oxygen concentration than the river water, and this will increase the estimate of community respiration (CR) while decreasing the estimate of gross primary productivity (GPP) (Hall and Tank 2005). The level of bias can be quite high, with a 10% increase in groundwater discharge potentially biasing CR estimates 50% too high. It is possible to correct estimates of CR for this bias, provided the concentration of O_2 in the groundwater is known (Hall and Tank 2005). Fortunately, the bias in GPP estimates is independent of the O_2 concentration of groundwater, and therefore is easily corrected by knowing only groundwater inputs. We suggest that bias of GPP be corrected in all metabolism measurements, and that investigators attempt to correct bias in CR when potential for bias is >30%, since other errors in CR estimation are often that high (see below). Free-water metabolism estimates have several other sources of error (McCutchan et al. 1998). Estimates of O_2 concentration contain some error because electrodes may vary by a few percent of saturation. Streams with high rates of reaeration can be problematic because the O_2 concentrations in water will approach saturation, causing small variations in probes (e.g., 2%) to amount to large errors in metabolism. In contrast, streams with low reaeration rates have large, easily measured O_2 differences from saturation, but the estimate of metabolism is still dependent on the estimate of reaeration rates. We suggest that to minimize error in metabolism, nighttime O_2 concentrations should be at least below 95% saturation, and that the reaeration rate is known with high confidence.

There has been little error assessment of whole-ecosystem metabolism derived from free-water methods, although McCutchan et al. (1998) determined that metabolism estimates are sensitive to reaeration and O_2 measurement error. We have used data from the Two Ocean Lake Creek, Wyoming, from a single day (29 July 1999) to make a preliminary estimate of uncertainty. Oxygen concentration and temperature were measured at 10-min intervals throughout a 24-hr period at the top and bottom of a stream reach with an average travel time of 16.2 min. The

reaeration was estimated to average 0.0257 min^{-1} , when corrected for temperature. We assumed that O_2 probes were accurate to within 2% and that a probe deviated from the ideal calibration consistently throughout the day. All the elements of the equation to estimate community metabolism (see chap.10, this volume), except depth, were assumed to vary normally about a mean (table 12.5) and were randomly combined 10,000 times for each time interval. Community respiration was estimated by scaling nighttime estimates to 24 hr; and to calculate GPP, average respiration was subtracted from the daytime metabolism estimates, which were then summed. We therefore assumed a positive correlation among the sampling intervals. Mean CR was estimated to be $-9.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, with a 95% confidence interval ranging from -6.2 to $-12.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$. Mean GPP estimate was $1.84 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ with lower and upper 95% confidence levels of 1.34 and $2.34 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively. This analysis indicates that for this reach and day, GPP was within $\pm 27\%$ and CR within $\pm 32\%$.

Summary

We encourage ecological researchers to address and quantify the uncertainty in NPP estimates to the extent possible from known sources of variability in their study systems. These analyses can be useful, not only to provide a sense of the reliability of the production estimates but also to aid in comparisons among sites and to help focus future work where additional efforts will be most fruitful in reducing uncertainty. In the interests of promoting "principles and standards," we have described common contributing factors and outlined several basic approaches to quantifying NPP uncertainty. However, as the examples above demonstrate, their application to particular biomes requires adaptation to particular sets of measurement variables and study designs.

Table 12.5. Estimates of error and uncertainty for GPP for a reach of Two Ocean Lake Creek, using the two-station method

Source of Error	Mean over 24 Hrs	Standard Deviation	Unit
O_2 probe			
O_2 saturation	80.19	0.5	%
O_2 concentration	6.67	0.05	mg l^{-1}
Reaeration rate	0.0257	0.00385	Minute^{-1}
Travel time	16.2	0.01	Minutes
Temperature	12.66	0.1	C
GPP mean	1.8405	0.2513	$\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$
GPP CV	13.65		%

Notes: Although the parameter value for each 10-min time interval was used, the mean of the value is given to indicate the relative level of variation. The uncertainty was determined by running each of the 191 time intervals 10,000 times, assuming a normal distribution.

Sources: Chapter 10, this volume; Hall and Tank (2003).

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