

Uncertainty in Calculations of Net Primary Production for Grasslands

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ABSTRACT

Net primary production (NPP) is a fundamental characteristic of all ecosystems and foundational to understanding the fluxes of energy and nutrients. Because NPP cannot be measured directly, researchers use field-measured surrogates as input variables in various equations designed to estimate 'true NPP'. This has led to considerable debate concerning which equations most accurately estimate 'true NPP'. This debate has influenced efforts to assess NPP in grasslands, with researchers often advocating more complex equations to avoid underestimation. However, this approach ignores the increase in statistical error associated with NPP estimates as a greater number of parameters and more complex mathematical functions are introduced into the equation. Using published grassland data and Monte Carlo simulation techniques, we assessed the relative variability in NPP estimates obtained using six different NPP estimation equations that varied in both the number of parameters and intricacy of mathematical operations. Our results indicated that more complex equations may result in greater uncertainty without reducing the probability of underestimation. 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. For example, due to greater variability in the field-measured belowground data than aboveground data, estimates of belowground NPP tended to have more uncertainty than estimates of aboveground NPP. An analysis in which the input data were standardized allowed us to isolate the details of the calculations from the variability in the data in assessing the propagation of uncertainty. This analysis made clear that equations with product terms have the potential to magnify the uncertainty of the inputs in the estimates of NPP although this relationship was complicated by interactions with data variability and number of parameters. Our results suggest that more complex NPP estimation equations can increase uncertainty without necessarily reducing risk of underestimation. Because estimates can never be tested by comparison to "true NPP", we recommend that researchers include an assessment of propagation of statistical error when evaluating the 'best' estimation method.

Key words: NPP; ANPP; BNPP; methods of calculating net primary production; uncertainty in calculations of NPP; Monte Carlo simulation; uncertainty analysis; grassland; underestimation.

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INTRODUCTION

Net primary production (NPP) is a key characteristic of all ecosystems and is fundamental to understanding of their ecology and biogeochemis-

try. It represents the amount of biomass, energy, or carbon fixed by autotrophs in excess of their respiratory needs and therefore available to higher trophic levels. It is also the source of the organic carbon stored in ecosystems to which important nutrients such as nitrogen are bound.

Although there is unanimity in the ecological community about the definition of NPP (gross photosynthesis minus plant respiration), no such consensus exists for the preferred methods of calculation of NPP from field data. Because the terms in the definition of NPP cannot be directly measured under field conditions, assumed mathematical relationships between proxy measures and NPP are required. This has led to a large number of estimation methods, none of which have received universal acceptance (Milner and Hughes 1968; Singh and others 1975; Linthurst and Reimold 1978; Sala and Austin 2000; Lauenroth 2000; Scurlock and others 2002). Failure to identify a universally accepted method hinges on disagreements about the type and number of proxy measures that should be included in NPP calculations. Discussions of the advantages and disadvantages of different methods of calculation began essentially as soon as estimates of NPP began to be published (Odum 1960; Milner and Hughes 1970; Singh and others 1975). Although the controversy has arisen around estimates of NPP from all ecosystem types, nowhere has it been more detailed than in grasslands (Singh and others 1975; Scurlock and others 2002).

The grassland NPP discussion has focused almost entirely on the degree to which various methods of calculation underestimate "true NPP". Although "true NPP" is unknowable, conclusions about the degree of underestimation have been reached by comparing particular methods of calculation with the conceptual components in the definition of NPP. This has led to discussions dominated by comparisons of the numbers of components used in the calculation and to a large extent criticism of simple in favor of complex estimates (Singh and others 1975; Linthurst and Reimold 1978; Scurlock and others 2002).

Given that true NPP is unknowable, at least with current technology, the 'underestimation' arguments are self-evident and almost beyond challenge. To date, the only effective challenges have been sample-frequency counter arguments (Singh and others 1984; Lauenroth and others 1986; Sala and others 1988; Biondini and others 1991). These analyses demonstrated that attempts to resolve small differences in biomass (between two dates) can lead to substantial error in estimates of NPP

both positive and negative (see Sala and Austin 2000 for a detailed example), which suggests that underestimation should not be our only concern in estimating NPP. Furthermore, because most methods of calculation ignore negative increments in biomass they have a guaranteed positive bias (Biondini and others 1991).

With the exception of the sample-frequency analyses, there has been little consideration of statistical error or uncertainty associated with estimates of NPP (Linthurst and Reimold 1978; Lauenroth 2000). All of the 'underestimation' arguments assume that there is no uncertainty cost coupled with increasing the number of parameters in the calculation of NPP. Hence complex methods of calculation that require more variables have been suggested to be preferable to simple methods with fewer parameters (for example, Scurlock and others 2002). Although this approach is consistent with the objective of choosing a method of calculation that is as close to the concept of NPP as possible, it runs the risk of being subject to the well known bias-variance tradeoff (Burnham and Anderson 2002). Predictive error consists of two parts: bias and variance; increasing the complexity of a model or method of calculation can decrease bias, but the result is often an increase in variance of the outcome (Burnham and Anderson 2002).

Our objective for this paper is to evaluate the relationship between the complexity of the calculation used to estimate NPP and the uncertainty associated with the estimate. We hypothesized a positive relationship between the complexity of the calculation and the amount of uncertainty in the estimate of NPP as a result of the propagation of uncertainty from the input data through the calculations.

Our approach had two components. The first was to appraise uncertainty using a range of methods of calculation and a real data set from a grassland. The second was a standardized analysis that entailed constructing a data set that consisted of input variables with the same magnitudes, but incremental variability. This allowed us to separate the particular characteristics of the data set from the variance-propagating properties of the methods of calculation.

METHODS

Net primary production is not a directly observable characteristic of an ecosystem. Consequently, approaches to estimating NPP consist of a collection of methods to approximate the amount of biomass or carbon that autotrophs assimilate over a particular

time interval. Each method consists of a technique to collect the relevant information in the field and an assumed mathematical relationship between the proxy variable(s) sampled in the field and NPP.

Conceptually, NPP during the interval from $t = 1$ to $t = 2$ is:

$$\text{NPP} = \Delta B + \Delta H + \Delta E + \Delta D + \Delta V, \quad (1)$$

where ΔB is the change in biomass, ΔH is the amount of biomass consumed by herbivores, ΔE is the amount of biomass lost to exudation, sloughing, and transfers to symbionts and parasites, ΔD is the amount of biomass lost to death and detachment, and ΔV is volatile losses of organic compounds—all during the interval $t = 1$ to $t = 2$. All of the methods to estimate NPP are designed to approximate one or more of the terms on the right hand side of equation (1). In practice, each method is applied to either above- or belowground NPP separately. Often in a single study, the methods used for above- and belowground NPP address different numbers of the components in equation (1).

Estimating NPP

We selected a set of commonly used methods that can be applied to either above- or belowground NPP and that have recently been evaluated by Scurlock and others (2002). We used six of the seven methods described by Scurlock and others (2002), and in their numbering scheme, we used methods 1, 2, 3, 4, 6, and 7. We will refer to them as methods numbered 1–6. Method 1 assumes that NPP can be estimated by peak live biomass. Method 2 associates peak standing crop (live plus dead) with NPP. The key assumption here is that some of the biomass produced during the interval of interest may senesce before sampling. Method 3 uses the difference between the minimum and maximum estimates of live biomass as an estimate of NPP. The key assumptions are that some live material is carried over from previous intervals and that there is a single peak in live biomass. Method 4 sums all of the positive increments in live biomass to estimate NPP. It assumes that live material is carried over from previous seasons and that there may be multiple peaks in live biomass during the interval. Method 5 uses the sum of positive increments in live biomass, standing dead biomass, and litter to estimate NPP. If an increment in live biomass also corresponds to an increment in total dead (standing dead + litter) the entire increment is counted (increment in live and increment in total dead). This method makes the same assumptions as

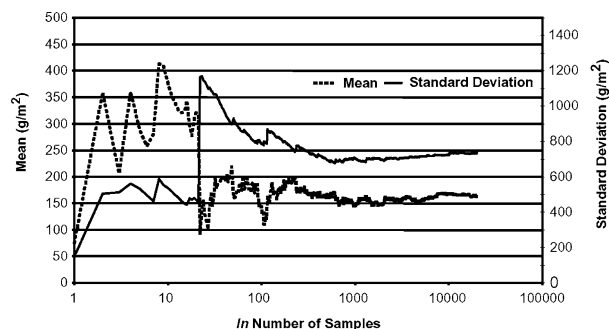


Figure 1. Relationship between the number of samples and the mean and standard deviation of belowground dead material in 1987.

method 4 with the additional assumption that live material may be transferred to the dead or to the litter during the interval of interest. Method 6 sums the changes in live and dead biomass (positive or negative) and adds to that the amount of material that decomposed during the interval. The additional assumption is that not only can live material be transferred to the litter but that some of it may decompose during the interval. In terms of equation (1), all of the methods focus on ΔB (biomass) and ΔD (death and detachment) and ignore ΔH (herbivory) and ΔE (exudation and sloughing). To the extent that herbivory, exudation, and sloughing are important, all of the methods have the potential to underestimate “true NPP”.

Biomass Data

The data for our analysis are from a grassland near Mexico City, Mexico. The Chapingo site is located approximately 20 km northeast of Mexico City ($19^{\circ}27'30''\text{N}$, $98^{\circ}54'30''\text{W}$) at 2,241 m elevation (Garcia-Moya and Castro 1992). Mean annual precipitation is 579 mm most of which falls during a 6 month wet season from May to October. Mean annual temperature is 15.1°C and the mean temperature in January (the coldest month) is 11.6°C .

The data can be found in Figure 3.4 in Garcia-Moya and Castro (1992). Data were collected in the original study between September 1984 and December 1987. Because of a fire at the study site, there were 2 months of missing data during 1986. Therefore, we used data only for the years 1985 and 1987, which had complete monthly data. We extracted the monthly values by laying a grid over the bar charts and reading the values from the y-axes. To check our values, we compared them to the numbers reported in the text of (Garcia-Moya and Castro 1992). Our numbers were never different by more than 0.5% from those reported in the text.

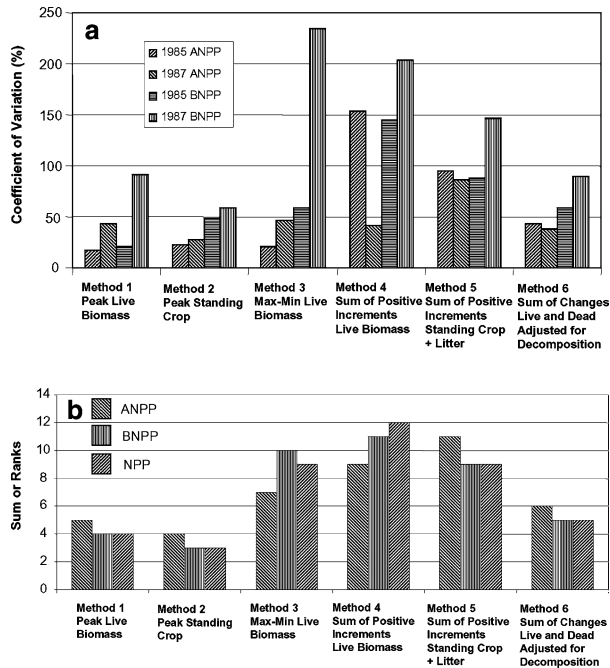


Figure 2. Variability associated with estimates of aboveground net primary production (ANPP) and belowground net primary production (BNPP) over 2 years for six methods of calculation from field data; **a** coefficients of variation (CV), **b** ranked variability. Ranked variability was calculated by assigning a 1 (smallest CV) through 6 (largest CV) to each of the methods for ANPP, BNPP, and NPP for both years. The ranks were summed across years for ANPP, BNPP, and NPP.

The data consisted of monthly means and standard deviations for above- and belowground live biomass, dead biomass, and decomposition all in g/m^2 . Aboveground live and dead biomass were collected by clipping $0.25 m^2$ rectangular quadrats. Belowground biomass was collected with a 10-cm deep \times 7.5-cm diameter soil core. Live and dead roots were separated using tetrazolium chloride and hand sorting. Decomposition was estimated with $3 cm \times 2 cm$ litter bags with a mesh size of 2 mm. The bags were installed both above- and belowground (5-cm deep).

Monte Carlo Analysis

Monte Carlo analysis is an effective method of propagating uncertainty (variability) through a set of calculations such as those used to estimate NPP in grasslands (O'Neill 1973; Gardner and O'Neill 1981; O'Neill and others 1982). Our approach was to use the mean and standard deviation of each input variable to generate a distribution of input variables. The mean and standard deviation for

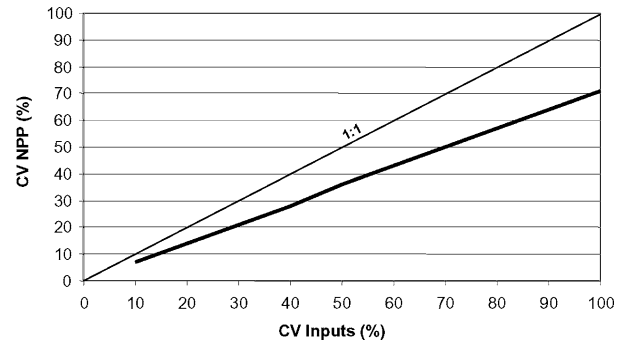


Figure 3. Relationship between the CV of input data and the CV of estimated NPP for method 5—sum of positive increments in standing crop + litter.

each variable was entered into a log normal random number generator to generate 20,000 random estimates. Because many of the means were associated with large standard deviations, we chose to use the log normal distribution to guarantee that all of our random values were equal to or greater than zero. To generate random numbers we used PopTools, a Microsoft Excel add-in developed by Greg Hood at the Pest Animal Control Cooperative Research Centre, based at Wildlife and Ecology, CSIRO, Canberra, Australia. After generating 20,000 values of each input variable, we calculated 20,000 estimates of aboveground NPP (ANPP) and belowground NPP (BNPP) for each of our six methods. For a detailed example of such calculations, see Table 4.4 in Lauenroth (2000). From our 20,000 estimates of ANPP and BNPP for each method we then calculated a mean, standard deviation, and coefficient of variation (CV). Finally, we combined ANPP and BNPP to calculate the same statistics for NPP.

To assess whether 20,000 samples were adequate, we visually inspected the cumulative means and standard deviations of our input variables. As an example, the annual change in the amount of belowground dead material for 1987 was one of the most variable inputs. Our estimated mean, standard deviation and CV were $172 g/m^2$, $741 g/m^2$ and 431%, respectively. The variability in the cumulative mean and standard deviation began to stabilize near 10,000 samples and reached a stable value between 10,000 and 20,000 (Figure 1). These results provided us with confidence that our sampling scheme was adequate.

Standard Input Analysis

Because the Monte Carlo analysis relies upon and incorporates all of the variability found in the field data, we tested the variance propagation properties

Table 1. Means ($\text{g m}^{-2} \text{y}^{-1}$), Standard Deviations ($\text{g m}^{-2} \text{y}^{-1}$), and Coefficients of Variation (CV, %) for Estimates of Aboveground Net Primary Production (NPP) using Six Different Methods of Calculation

	Peak live biomass	Peak standing crop	Max-min live biomass	Sum of positive increments live biomass	Sum of positive increments standing crop + litter	Sum of changes live and dead adjusted for decomposition
1985						
Mean	316	1,287	265	164	1,031	864
Std Dev	54	283	56	251	965	371
CV	17	22	21	153	94	43
1987						
Mean	254	801	239	241	743	661
Std Dev	110	213	110	101	638	254
CV	43	27	46	42	86	38

The data are from a grassland in Chapingo, Mexico for 1985 and 1987 based upon data from Garcia-Moya and Castro (1992). The methods are described in more detail in the text.

Table 2. Means ($\text{g m}^{-2} \text{y}^{-1}$), Standard Deviations ($\text{g m}^{-2} \text{y}^{-1}$), and CV (%) for Estimates of Belowground NPP using Six Different Methods of Calculation

	Peak live biomass	Peak standing crop	Max-min live biomass	Sum of positive increments live biomass	Sum of positive increments standing crop + litter	Sum of changes live and dead adjusted for decomposition
1985						
Mean	746	1,703	481	850	2,076	924
Std Dev	155	814	283	1,236	1,828	534
CV	21	48	59	145	88	58
1987						
Mean	690	1,694	387	969	1,738	1,199
Std Dev	631	976	912	1,973	2,555	1,064
CV	91	58	235	204	147	89

The data are from a grassland in Chapingo, Mexico for 1985 and 1987 based upon data from Garcia-Moya and Castro (1992). The methods are described in more detail in the text.

for three of the methods by using a standard set of calculations. We tested methods 2, 5 and 6 by choosing a set of input variables with the same magnitudes and increasing the CV of inputs from 10 to 100% in increments of 10%. This allowed us to methodically evaluate the relationship between the variability of the input data and the variability of the results.

RESULTS

Chapingo Biomass Data

Garcia-Moya and Castro (1992) reported annual NPP of 1,994 and 1,611 g/m^2 for 1985 and 1987, respectively, at Chapingo (method 6). Our calculations from their data using method 6 resulted in estimates of 1,788 and 1,860 g/m^2 . The differences between our estimates and theirs are very likely the result of Garcia-Moya and Castro having used a

3-month weighted moving average to decrease the variability of their data before they calculated NPP. Garcia-Moya and Castro calculated the mean for any month i as a linear combination of month $i-1$, month i , and month $i+1$ using the following equation:

$$X''_t = 0.25X_{t-1} + 0.5X_t + 0.25X_{t+1}, \quad (2)$$

where X'_t is the smoothed mean for month t and X_t is the untransformed mean for month i . Such smoothing has the effect of flattening peaks in biomass.

Our range of methods of calculation produced a huge range of values for both the means and standard deviations for ANPP (Table 1), BNPP (Table 2) and NPP (Table 3). Because of the large differences in means among methods, our comparisons of uncertainty will rely on CV rather than standard deviations. The CV expresses relative

Table 3. Means ($\text{g m}^{-2} \text{y}^{-1}$), Standard Deviations ($\text{g m}^{-2} \text{y}^{-1}$), and CV (%) for Estimates of NPP using Six Different Methods of Calculation

	Peak live biomass	Peak standing crop	Max-min live biomass	Sum of positive increments live biomass	Sum of positive increments standing crop + litter	Sum of changes live and dead adjusted for decomposition
1985						
Mean	1,062	2,990	746	1,014	3,107	1,788
Std Dev	164	862	288	1,261	2,067	650
CV	15	29	39	124	67	36
1987						
Mean	944	2,495	626	1,210	2,481	1,860
Std Dev	641	999	919	1,976	2,633	1,093
CV	68	40	147	163	106	59

The data are from a grassland in Chapingo, Mexico for 1985 and 1987 based upon data from Garcia-Moya and Castro (1992). The methods are described in more detail in the text.

variability by dividing the standard deviation by the mean, making the CV more comparable across results. Our estimates of ANPP for 1985 ranged from a low of 164 g/m^2 by method 4 to a high of $1,287 \text{ g/m}^2$ using method 2 (Table 1). In 1987, ANPP varied from 239 g/m^2 by method 3 to 801 g/m^2 by method 2. BNPP ranged from $481\text{--}2,076 \text{ g/m}^2$ in 1985 to $387\text{--}1,738 \text{ g/m}^2$ in 1987. The lowest estimates of BNPP were obtained by method 3 and the highest by method 5, whereas methods 3 and 4 produced the lowest ANPP estimates and method 2 the highest. The results for NPP corresponded to the ANPP and BNPP results. Method 3 produced the lowest estimates and methods 2 and 5 the highest.

Although methods 2 and 5 consistently produced the largest estimates of net production, they did not have the greatest amount of uncertainty (Figure 2a). In three of the four comparisons, method 4 had the largest CV for each of the ANPP and BNPP estimates. But neither method 4 nor method 5 produced the largest CV. BNPP by method 3 in 1987 had a mean of 387 g/m^2 with a CV of 235%. Consistently, CVs associated with the estimates of method 2 were among the lowest. Ranking the methods from 1 (lowest CV) to 6 (highest CV) and summing the ranks across years indicated that methods 3, 4, and 5 had the greatest amount of uncertainty associated with their estimates of ANPP, BNPP and NPP (Figure 2b). Methods 1 and 2 had the lowest uncertainty and method 6 was intermediate.

Standardized Biomass Data

Standard input and incremental variability indicated that the variability of method 2, peak

standing crop, was exactly equal to the variability in the input data. The equation for method 2 is:

$$\text{NPP} = \text{MAX } \text{SC}_t \text{ for } t=1, 2, 3, \dots, n, \quad (3)$$

where SC_t is standing crop measured on the t th sampling date. Because SC is the only input, the variability of the estimate of NPP was equal to the variability of SC. Method 5 produced the most variable estimates of NPP from field data and standard analysis indicated that the calculations attenuate variability such that the variance of NPP is guaranteed to be equal to or less than the variance of the input data depending upon whether a positive increment in total dead is added to the positive increment in live. The equation for method 5 requires a decision based upon whether a positive increment in dead material is simultaneous with a positive increment in live biomass. The equation is:

$$\text{NPP} = \Sigma(\text{PL}_t + \text{PD}_t) \text{ for } t=1, 2, 3, \dots, n, \quad (4)$$

where PL_t is the positive increment in live biomass between the t th and t th - 1 sample dates and PD_t is the corresponding positive increment in dead biomass. If there is a simultaneous increment in dead the equation is solved as stated. If there is no increment in dead, the PD_t 's drop out and NPP is the sum of positive increments in live biomass. If the estimate is composed of just positive increments in live, the variance of NPP will be equal to the variance of the sum of live increments. In terms of Figure 3, this case would fall on the 1:1 line. If there are simultaneous positive increments in total dead then the variance of NPP may be larger than the variance of the input variables by a factor of 2. The standard deviation of NPP will increase as a factor of the $\sqrt{2}$. Therefore the relative variability

(CV) of NPP will increase more slowly than the CV of the input variables (Figure 3).

Method 6 had intermediate variability in our analysis of the Chapingo data, but a complex response to standard analysis. The equation for method 6 is different from the other equations in that it contains a multiplication process as well as addition. The equation is:

$$\text{NPP} = \Sigma L_t + \Sigma D_t + \Sigma k_t D_t \quad \text{for } t = 1, 2, 3, \dots, n, \quad (5)$$

where L_t and D_t are live and dead biomass on the t th sample date and k_t is the decomposition rate during the interval t to $t-1$. Decomposition contributed an average of 60% to NPP at the Chapingo site resulting in essentially a 1:1 transfer of the variability in the input variable to uncertainty in the estimate of NPP.

DISCUSSION

All of our estimates of NPP had considerable uncertainty associated with them, but there was not a simple relationship between the complexity of the calculation of NPP and the amount of uncertainty. This finding leads us to reject our hypothesis that there is a clear positive relationship between the complexity of the method of calculation and the amount of uncertainty. The results of our analysis of the Chapingo data set suggested that the amount of variability of the specific input variables used in the calculation was more important than the number of variables used in the calculation or the specific mathematical operations. By standardizing the analysis and controlling for the relative variability of the input variables, we identified a method that simply transmitted the variability of the inputs to the output (method 2), one that attenuated the input variability (method 5), and one that has the potential to amplify the variability (method 6).

Our calculations confirmed what others have reported: different methods of calculation using the same data set produce different estimates of NPP (Tables 1, 2, 3) (Singh and others 1975; Linthurst and Reimold 1978; Dai and Wiegert 1996; Scurlock and others 2002). The new result from our analysis is the extensive variability in the amount of uncertainty associated with each of the estimates. Method 2 produced the largest estimates of ANPP for both years and comparatively low uncertainty. All of the methods for BNPP had higher uncertainty than for ANPP reflecting the more variable belowground data. The largest estimates of BNPP had CVs ranging from 50% to greater than 200%. Although the more complex methods tended to produce large

estimates, they also tended to have the greatest uncertainty. The same was true for NPP. Throughout our analysis, method 2 was an exception to the general trend. It consistently produced estimates close to those obtained by more complex methods thought to minimize the probability of underestimation yet with substantially less uncertainty. Scurlock and others (2002) compared six methods of calculation from simple to complex for five ecoregions and found that method 2 (peak standing crop) produced estimates of ANPP and BNPP that were equal to or greater than the other five methods. By contrast, Linthurst and Reimold (1978) reported that peak standing crop produced low estimates of ANPP in 14 of their 16 comparisons.

Our standard analysis that controlled for relative variability in the input data made it possible to identify how the mathematical operations included in the calculations contributed to propagating uncertainty. Uncertainty in estimates of NPP from methods that use a single input variable, such as methods 1 and 2, will directly reflect the uncertainty in the input data. The explanation for why these tended to have low uncertainty in our analysis is associated with the fact that live and total standing crop are relatively easy to estimate with low variability, especially aboveground. When the calculations include sums or differences of components, such as with methods 3, 4 and 5, the uncertainty in the estimate of NPP will always be less than the average uncertainty in the input data (Figure 3) assuming zero covariance. The large CVs for BNPP by these methods reflect the huge amount of variability in the belowground input data. This was particularly true for belowground live biomass. Calculations that include combinations of sums and products to produce estimates of NPP such as method 6 can produce reduced or expanded uncertainty in the results compared to the inputs depending upon the relative importance of the sum and product in the result (Figure 4). If the sum dominates the estimate of NPP, the uncertainty in the input data will be attenuated. If the product dominates, the uncertainty will be amplified (Figure 5). Analysis of method 6 indicated that the crossover point between attenuation and amplification occurs at the point when the decomposition term accounts for 56% of the estimate of NPP. It is ironic that the ecosystems for which this method was designed, those with a high intraseasonal turnover in biomass, are the ones that will have the highest probability of large uncertainty associated with estimates of NPP. For example, in a grassland in which the decomposi-

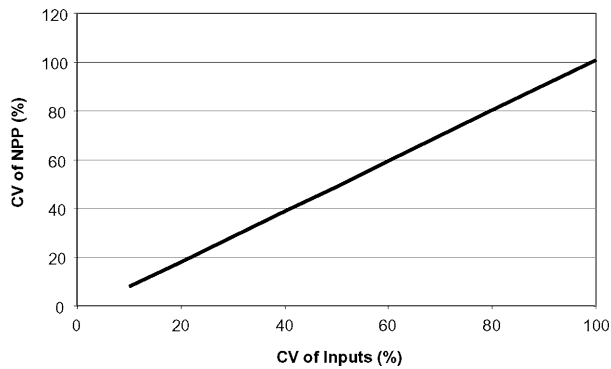


Figure 4. Relationship between the CV of input data and the CV of estimated NPP for method 6—sum of changes in live and dead adjusted for decomposition.

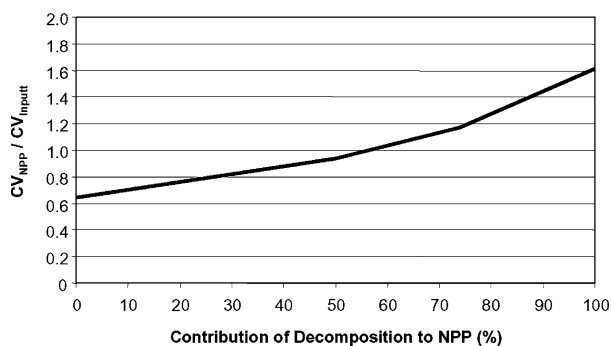


Figure 5. The relationship between the percentage contribution of decomposition to NPP and the ratio of the CV of the input variables to the CV of the estimate of NPP by method 6.

tion term accounts for 90% of the estimate of NPP, the uncertainty associated with the estimate will be 140% of the CV of the input data.

What do our results suggest about underestimation of NPP? Scurlock and others (2002) made the assumption that the larger estimates of more complex methods were evidence that simpler methods underestimated NPP, and therefore complex methods were to be preferred. Although there is agreement that simple methods have the potential to underestimate NPP, there is less agreement that complex methods are always better (Linthurst and Reimold 1978; Dai and Wiegert 1996). For instance, researchers in tidal marshes have concluded that methods using an estimate of loss of dead material (method 6) often result in overestimates of NPP (Linthurst and Reimold 1978; Dickerman and others 1986; Dai and Wiegert 1996). Our finding that method 2 produced estimates of NPP equal to or greater than the more complex methods either adds confusion to the discussion of

underestimation or more appropriately emphasizes that comparative analysis of field data is likely to add little to the issue of underestimation. The question of bias in methods of estimating NPP has been explored previously and found to be complex (Singh and others 1984; Lauenroth and others 1984; Sala and others 1988; Raich and Nadlehoffer 1992). Two conclusions can be extracted from this work. The first is that a positive bias introduced by ignoring “negative production” influences effectively all of our estimates of NPP (Singh and others 1984; Sala and others 1988; Raich and Nadlehoffer 1992). The second is that sample variance and sampling frequency can interact to produce large overestimates using methods that in the absence of sample variance are known to underestimate NPP (Singh and others 1984; Lauenroth and others 1984). Additional analyses using simulation models with known NPP (Singh and others 1984; Lauenroth and others 1984) or with the application of conceptual constraints (Raich and Nadlehoffer 1992) is likely to aid us in both understanding and detecting bias in estimates of NPP, but we may never have a satisfactory answer to the question of what is the best method to estimate NPP.

Because NPP is a conceptual, not a measurable, attribute of ecosystems, the answer to the “best method” or “underestimation” question is best left in the conceptual realm constrained by the objective of the particular investigation. What our results have added to the underestimation discussion is the reminder that each additional variable estimated from field data included in a calculation of NPP comes with an amount of uncertainty that will be transferred through the calculations. Whether the uncertainty will be amplified or attenuated will depend on the nature of the calculations, although our results for Chapingo suggested that the exact nature of the transfer can be complex.

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