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Estimating annual bole biomass production using uncertainty analysis

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Abstract

Two common sampling methodologies coupled with a simple statistical model were evaluated to determine the accuracy and precision of annual bole biomass production (BBP) and inter-annual variability estimates using this type of approach. We performed an uncertainty analysis using Monte Carlo methods in conjunction with radial growth core data from trees in three Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominated sites (young, mature, and old-growth) in the western Cascades of Oregon. A model based on the mean and standard deviation of annual radial growth from sampled trees was used with and without stratification by tree size to predict radial growth for non-sampled trees. Sample sizes of 64–128 trees per stand were required to achieve accuracy and precision within $\pm 10\%$. Without stratification the model underestimated annual BBP (Mg ha^{-1} year^{-1}) in all three age classes by up to 28%, and inter-annual variability by as much as 26%. Applying stratification increased accuracy of estimates at least twofold, and precision of estimates improved by 3–10%, resulting in decreased sample size requirements. The coefficient of variation of error of estimates was half that of inter-annual variability over the study period. Thus, this approach can be used to examine patterns of inter-annual variability of BBP in response to changing climate and land use patterns.

1. Introduction

The role of forests in the global carbon cycle, and their ability to act as future sources or sinks of atmospheric carbon in relation to climate change and land use (Dixon et al., 1994; Clark et al., 2001) has been a topic of extensive research for over two decades (Webb et al., 1983; Graumlich et al., 1989; Turner and Koerper, 1995; Schimel et al., 2000; Turner et al., 2000; Clark et al., 2001; Knapp and Smith, 2001; Law et al., 2003; Huxman et al., 2004). Net primary productivity (NPP) plays a significant role in determining carbon storage in forests, and the variability and behavior of NPP has implications for ecosystem response to future changes in climate (Knapp and Smith, 2001). Determining the variability of NPP at an annual time scale over a considerable spatial extent (landscape to region) could lend insights to temporal behaviors that affect ecosystem responses.

The production of woody tissue by trees is a large component of NPP in forests (Ryan et al., 1997), contributing approximately 25–30% of aboveground NPP in forest of the Pacific Northwest (Grier and Logan, 1977; Harmon et al., 2004). Several approaches are used to measure components of NPP in forests (Clark et al., 2001). Site-level estimates of NPP from ground-based measurements are likely to be the most accurate and precise, but can be costly, making sampling large spatial extents with an annual temporal resolution prohibitively expensive. Permanent study plots (Acker et al., 1998) have been used to measure growth and mortality to estimate long-term trends in NPP (Acker et al., 2000, 2002), although the long measurement intervals do not lend themselves to accurate and precise annual estimates, nor estimates of inter-annual variability. Some studies have measured and examined annual NPP on small spatial scales by collecting tree cores from small plots (<0.1 ha) in which all trees (e.g., Graumlich et al., 1989) could be sampled. Alternatively a sub-sample of tree cores can be taken (Campbell et al., 2004), although the sample sizes and their effect on accuracy and precision of estimates are generally not reported in the literature. These small plot-based approaches are also difficult to apply over larger spatial scales

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Table 1
Site characteristics for three low-elevation conifer sites in the western Cascades of Oregon used to investigate sampling and modeling methodology for estimating annual bole biomass production

Characteristic	Site		
	RS07	RS32	WS06
Site location (latitude and longitude)	44°13′ N 122°15′W	44°44′ N 122°12′W	44°16′ N 122°11′W
Elevation (m)	460	650	900–1000
Age class (years)	Old-growth (450)	Mature (145)	Young (35)
Dominant tree species	Douglas-fir/western hemlock	Douglas-fir/western hemlock	Douglas-fir
Area sampled (ha)	0.25	0.25	0.55
Stand density (trees/ha)	284	600	565

due to time and monetary costs, and can have limitations in estimating NPP (see Bond-Lamberty et al., 2004; Campbell et al., 2004).

In this paper we explore a method for using increment cores in combination with long-term permanent plots to estimate annual bole biomass production (BBP), and evaluate the effect of sample size, sampling methodology, and the use of a simple model on these estimates. Given that BBP (i.e., stem wood and bark production) is a large component of tree NPP (40–70%; Grier and Logan, 1977; Runyon et al., 1994; Campbell et al., 2004), we focused explicitly on production of biomass associated with tree boles (defined here as production of stem wood plus bark). With this analysis we evaluated methods of sub-sampling trees and modeling annual radial growth to estimate annual tree BBP and to examine the uncertainty associated with these estimates. We applied two commonly used sampling methodologies coupled with a simple statistical model based on the mean and standard deviation of annual radial growth. Estimates derived from this method can then be used in related studies to ask questions regarding climatic variability and behaviors of annual NPP across different spatial scales. This method may also be a viable approach for estimating annual NPP in other types of plots and forested regions. We specifically attempted to answer three questions: (1) what sub-sample sizes of tree increment cores are required to estimate annual BBP within ±10% accuracy and precision? (2) Is a simple model for radial growth prediction of non-sampled trees adequate to estimate site-level annual BBP for varying age classes with the desired level of accuracy and precision (i.e., ±10%)? (3) How can accuracy and precision of estimates of annual BBP be determined as a function of sample size? Using Monte Carlo methods in an analysis of uncertainty, we were able to understand the effect of sampling and modeling methodologies and sample size on the accuracy and precision of our estimates of annual BBP.

2. Materials and methods

2.1. Study area

Data were collected in three long-term permanent study plots within the H.J. Andrews Experimental Forest, Blue River, OR. The experimental forest covers a 6400 ha drainage located in the western Oregon Cascades. Elevation ranges from 410 to 1630 m. The maritime climate consists of cool wet winters and dry warm summers. Average annual precipitation ranges from 230 cm at lower elevations to 355 cm at higher elevations. Annual average daily temperatures range from 0.6 °C in January to 17.8 °C in July (Bierlmaier and McKee, 1989).

Each of the three permanent study plot sites represents a different age class (young, mature, and old-growth) with similar species composition (Table 1). ''Young'' refers to second-growth forests developing following clear-cut harvesting. The sites are of different elevations, but all three were within the *Tsuga heterophylla* (Raf.) Sarg. forest zone (Franklin and Dyrness, 1988). All three sites are part of a long-term permanent study plot network designed to monitor changes in forest composition, structure, and function in the Pacific Northwest (Acker et al., 1998). All sites were established prior to increment core sampling and measured for tree growth and mortality (all trees >5 cm dbh) at approximately 5-year intervals. The old-growth site (RS07) was sampled for increment cores in the summer of 2000 (Fraser, 2001), the young site (WS06) was sampled in the summer of 2001, while the mature site (RS32) was sampled in the summer of 2003. The old-growth and mature sites are each a single 0.25 ha square plot. The young site is a small watershed study area that contains transects with small (0.025 ha) circular sampling plots spaced at regular intervals. Although these sites were not randomly selected, they are representative of the age classes occurring in this forested landscape.

2.2. Data collection

Within the two reference stands (mature and old-growth), all live trees ≥5 cm diameter at breast height (DBH) were sampled. Within the young site, samples were taken from all live trees ≥5 cm in the north half of each upland plot and the half of each riparian plot in the direction away from the gauging station (22 plots total). Sampling consisted of coring a tree at breast height and recording DBH to the nearest 0.1 cm. In both the mature and old-growth sites, trees ≥10 cm DBH were cored twice, at approximate right angles (preferentially the side-slope and upslope sides of the tree). In the young site, only one core per tree was collected due to the smaller size of the trees. Increment cores were stored in paper straws and taken to the lab for preparation and measurement. Individual cores were mounted on routed blocks with wood glue and a flat readable surface was created using a belt sander. Increment cores were then measured for annual radial growth to the nearest 0.001 mm

using one of two methods. Cores from the old-growth site were measured by hand using a microscope, and radial growth was averaged between the two samples for trees ≥10 cm DBH. Mature and young sites were measured using WinDendro™ image analysis software. All cores from these two sites were scanned to obtain an image for measurement, and the image was then digitally archived.

2.3. Biomass calculation

Annual stem diameters for each individual tree within a site were calculated using DBH measurements at the time of sampling, combined with annual radial growth from tree cores. For example, stem diameter for 1998 was calculated by subtracting the radial growth in 1999 from the measured DBH in 1999. The 1998 diameter, in combination with 1998 radial growth, was then used to calculate diameter for 1997. Stem diameters (outside bark) of each year were used in bole biomass equations to estimate the annual bole biomass (mass in Mg of stem wood and stem bark only) of each tree using species-specific allometric equations (Appendix 1) from BIOPAK (Means et al., 1994). BIOPAK is a software package containing documented equations used to estimate plant components (e.g., leaf mass, leaf area, stem wood mass, and bark mass). Equations, developed specifically for use in the western Cascades, were in the following form, $\ln(BST) = \exp(B_0 + B_1 \ln(DBH))$. Where BST is the total biomass of the tree bole and DBH is the tree diameter at breast height. Annual tree bole biomass production (BBP) was

calculated for all trees sampled for each site, and was summed to determine the annual bole biomass production of each site (i.e., bole biomass change for all trees in Mg ha^{-1} year^{-1}). This quantity of annual BBP will be referred to as the "true" annual BBP, as all individuals within the population of interest (≥5 cm DBH) were sampled. This quantity was used to compare to modeled outcomes with different sample sizes to evaluate accuracy and precision in an analysis of uncertainty (Fig. 1).

2.4. Simulated sampling and radial growth prediction

Two sampling methodologies coupled with a simple model to predict radial growth of non-sampled trees were evaluated by examining the distribution of estimates produced by each using a Monte Carlo method (Fig. 1). Simulated random sampling of radial tree growth was accomplished by sampling the population of trees from each site using a uniform probability function (SAS v9.0). These sampled trees were used to estimate the mean and standard deviation for subsequent modeling of radial growth. Sample sizes of these three finite populations were greater than 10%, therefore a finite population correction factor was applied to standard deviation estimates (Thompson, 2002). All modeling and uncertainty analyses were conducted using SAS v9.0. A description of each model follows.

2.4.1. Simple random model (SR)

The simple random model (Eq. (1)) uses the mean growth rate of all sampled trees in a given year, and the variation about
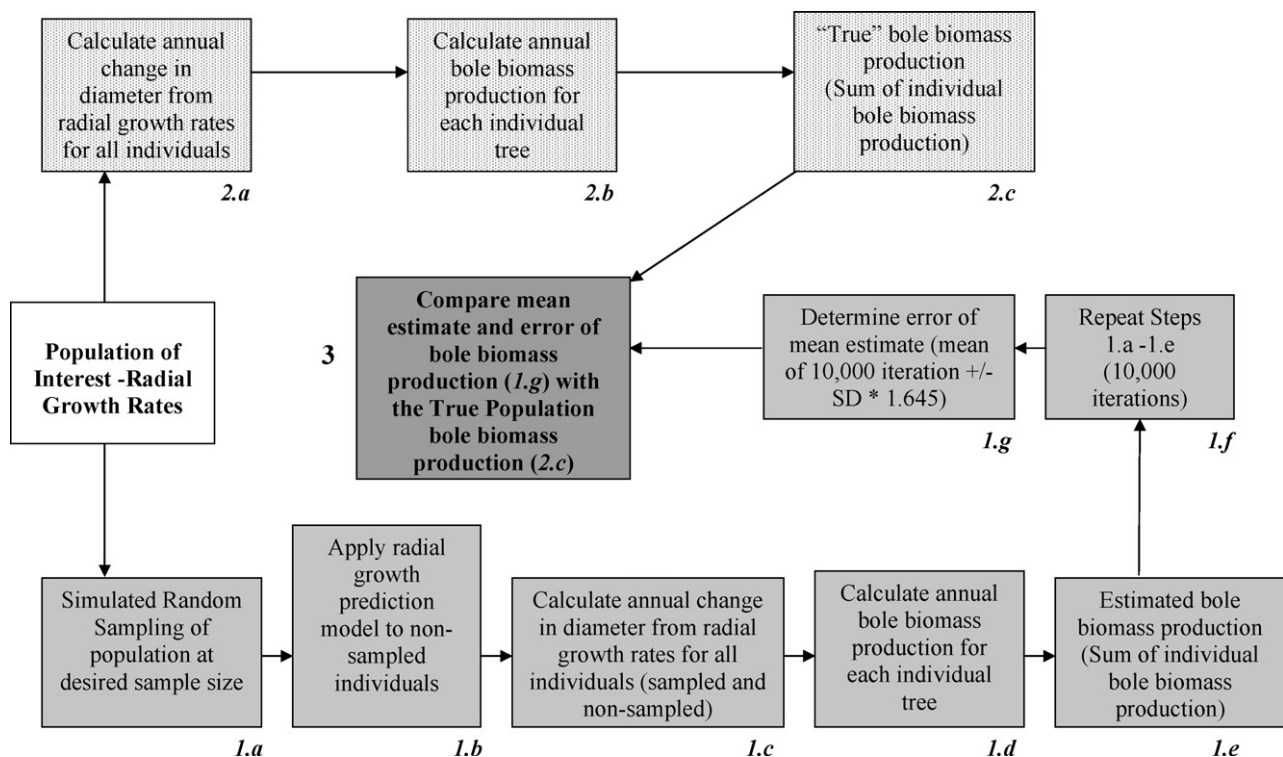

Fig. 1. Flow chart summarizing simulated random sampling and radial growth modeling using Monte Carlo simulations (1.a–1.g) to make comparisons (3) between estimates of bole biomass production and "true" bole biomass production (2.a–2.c).

that mean to predict radial growth for non-sampled trees:

$$\hat{G}_{ij} = \mu_j + \epsilon_{ij} \tag{1}$$

The radial growth ($\hat{G}_{ij}$) of a non-sampled tree (i) for a given year (j) is predicted by adding random variability (ϵ_{ij}) to the mean growth rate (μ_j) of sampled trees for that year. The random variability is based on the mean and variance (σ^2_{jq}) of the sampled distribution in that year. Without stratification by size class radial growth distributions for individual years did not meet the assumptions of normality (Shapiro–Wilk statistics 0.84–0.98; p-values ≤ 0.02).

2.4.2. Simple random stratified model (SRS)

The second model (Eq. (2)) applied stratified sampling and modeling of non-sampled individuals by tree size. Stratification resulted in radial growth distributions that more closely met the assumptions of normality (approximately half the tests exceeded the significance level of 0.05, whereas none exceeded this level without stratification). Simulated stratified sampling was accomplished by dividing the population into quartiles based on the most recent measurements of diameter, and each quartile was sampled separately using a uniform probability function (SAS v9.0). All calculations necessary for prediction, as well as the prediction of radial growth for non-sampled trees, were completed independently for each quartile.

$$\hat{G}_{ijq} = \mu_{jq} + \epsilon_{ijq} \tag{2}$$

The radial growth $\hat{G}_{ijq}$ of a non-sampled tree (i) for a given year (j) in quartile (q) is predicted by adding random variability (ϵ_{ijq}) to the mean growth rate (μ_{jq}) of sampled trees for year (j) and quartile (q). The random variability is based on the mean and variance (σ^2_{jq}) of the sampled distribution of year (j) for a given quartile (q).

2.5. Monte Carlo uncertainty analysis

To determine both accuracy and precision of estimates obtained from each model, an analysis of uncertainty was performed using Monte Carlo methods (Fig. 1). Simulated random sampling of radial growth from the population, radial growth modeling applications, and tree biomass calculations

were repeated 10,000 times, resulting in 10,000 estimates of site-level annual BBP (Mg ha^{-1} year^{-1}) for each sample size at each site. This number of iterations was necessary to provide normal distributions for further analysis.

Random sampling was conducted using a uniform distribution where all individuals had an equal probability of selection for each simulation. Simulated sampling sizes were 90%, 80%, 70%, 60%, 50%, 40%, 30%, 20%, and 10% of the entire population. The mean and standard deviation of these 10,000 estimates were used to compare to the "true" population annual BBP. The error of our mean estimate for a given model and sample size was calculated as the mean of the 10,000 estimates ±2 S.D. to capture 95% of the distribution of our estimates. This range was compared to a level of precision of ±10% of the "true" annual BBP.

3. Results

3.1. Simple random model (SR)

Results from the uncertainty analysis indicate that a simple random model (SR) underestimates annual BBP for all age classes (young, mature, and old-growth) at all sample sizes (Fig. 2 a, c, and e). For example, the mean estimate of annual BBP at the highest sample size fell below the "true" annual BBP of the entire population, for all sites in almost all years reported. Estimates for individual years at all three sites were 2–4% less than the "true" annual BBP at the highest sample size (90%) and 15–28% below at the lowest sample sizes (10%). The average annual BBP over all years (Table 2) was also underestimated by 0.388, 0.42, and 0.059 Mg ha^{-1} year^{-1}, for young, mature, and old-growth, respectively ("true" average annual BBP of 3.615, 4.359, and 3.461 Mg ha^{-1} year^{-1} for young, mature, and old-growth, respectively).

Linear regressions of estimates against the "true" annual BBP (Fig. 3 a, c, and e) illustrate an increasing bias in estimates as annual BBP increases for all three age classes. Results from simultaneous F-tests (Neter et al., 1983; Vanclay and Skovsgaard, 1997) indicate intercepts were statistically different from zero (p-value < 0.0001), and slopes were significantly different than one (p-value < 0.0001) for all three age classes. Therefore, the SR model was not as accurate

Table 2

Average annual bole biomass production and inter-annual variability of bole biomass production for model estimates and the entire population for three Douglas-fir sites in the western Oregon Cascades

	Estimate type	Young	Mature	Old-growth
Average BBP (Mg ha^{-1} year^{-1})	Entire population	3.615	4.359	3.461
	SR[a]	3.227	3.939	3.402
	SRS[a]	3.615	4.384	3.503
Inter-annual variability (Mg ha^{-1} year^{-1})[b]	Entire population	0.449	0.698	0.468
	SR[a]	0.333	0.589	0.442
	SRS[a]	0.437	0.644	0.464

Estimates of average annual bole biomass production (BBP) and inter-annual variability for old-growth and mature sites were based on a 32-year record, and estimates for the young site were based on a 12-year record.

[a] Sample sizes for these two model comparisons are 64 trees for the young and old-growth sites, and 128 trees for the mature site.

[b] Standard deviation of average bole biomass production over entire time series.
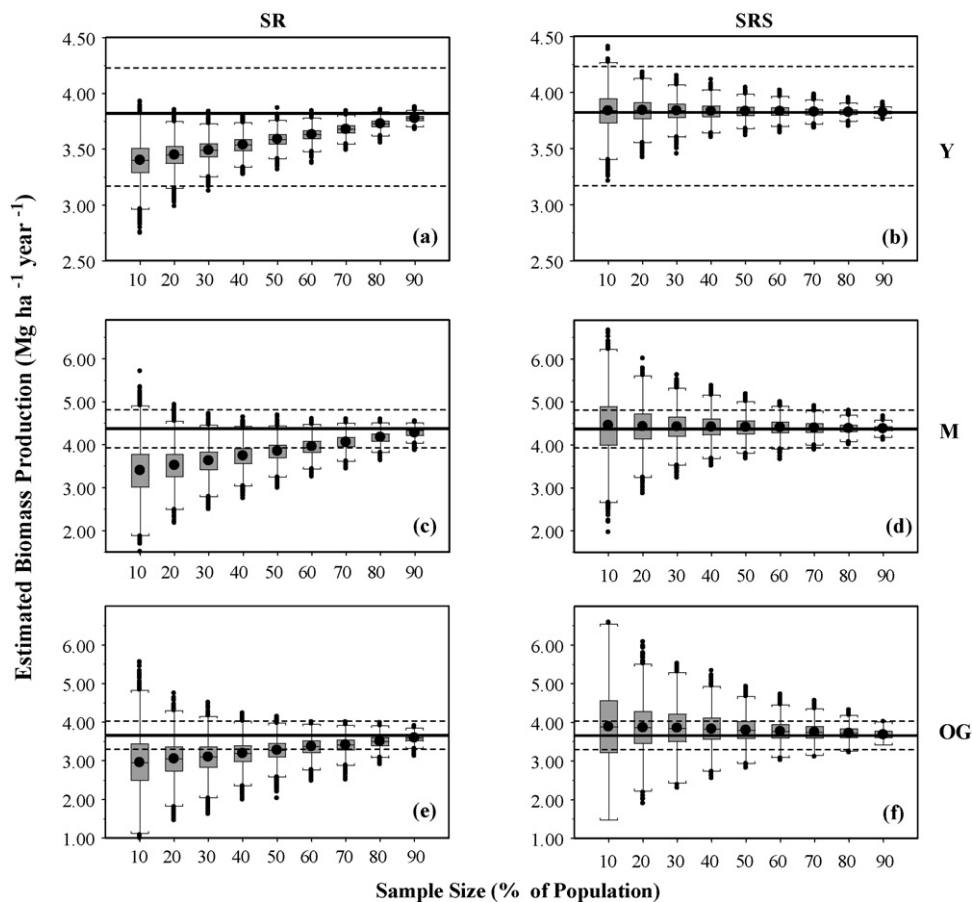
Fig. 2. Box plots showing distributions of bole biomass production estimates at varying sample sizes for both models, simple random (a, c and e) and stratified random (b, d and f) for an individual year (1995). Left and right panels are paired by age (Y = young a and b, M = mature c and d, and OG=old-growth e and f). Bold line indicates the "true" bole biomass production. Dashed lines are ±10% of "true" bole biomass production.

as desired, and the increasing bias as annual BBP increases (Fig. 3 a, c, and e) also led to underestimates of the inter-annual variability of average annual BBP (Table 2).

The SR model only met the desired level of precision (±10%) at the highest sample sizes for all three age classes. As expected, the precision of the estimates decreased (i.e., increased variability around the mean estimate of BBP annually) as sample sizes became smaller for all age classes (Fig. 2). The uncertainty analysis, however, did confirm that even with underestimation, the SR model was precise enough to be within ±10% for sample sizes ≥90% of the total population for each age class. The coefficient of variation (%CV) of estimates (error of estimate divided by the estimate) ranged from 3% to 4% across all three age classes. This was roughly one-fourth to one-third the %CV of the "true" annual BBP (average annual BBP divided by inter-annual variability) of 12.5 %, 16%, and 13.5% for the young, mature, and old-growth site, respectively. This result indicates the error of the BPP estimates was within the bounds of inter-annual variability.

3.2. Simple random stratified model (SRS)

The addition of stratification to sampling procedures and the simple random model resulted in improved accuracy of annual BBP estimates. For young, mature and old-growth sites, the SRS model estimated live annual BBP with a sample size of approximately 20%, 80%, and 90%, respectively, with a two to fourfold increase in accuracy over the SR model (Fig. 2 b, d, and f). The SRS model estimates necessitated a much larger sample size for the mature site than the young and old-growth sites for similar accuracy and comparable level of precision. These larger sample sizes were due to a loss of precision at lower levels of sampling, and not a large decrease in the accuracy of the estimate.

The range of estimates for the SRS model fell within ±10% of the "true" annual BBP with lower sample sizes than did estimates from the SR model for both the young and mature site, but not for the old-growth site (Fig. 2). The greater precision for the young and mature site was a result of lower standards deviations of estimates as compared to the SR model, while a slight decrease in precision (0.003–0.03 Mg ha^{-1} year^{-1}) of SRS model estimates for the old-growth led to similar sample size requirements for both models. As with the SR model, the precision of estimates from the SRS model decreased as sample size decreased.

The SRS model however, slightly overestimated the annual BBP for all age classes. Estimates of individual years among all three sites were 0.3–2% above the "true" annual BBP at
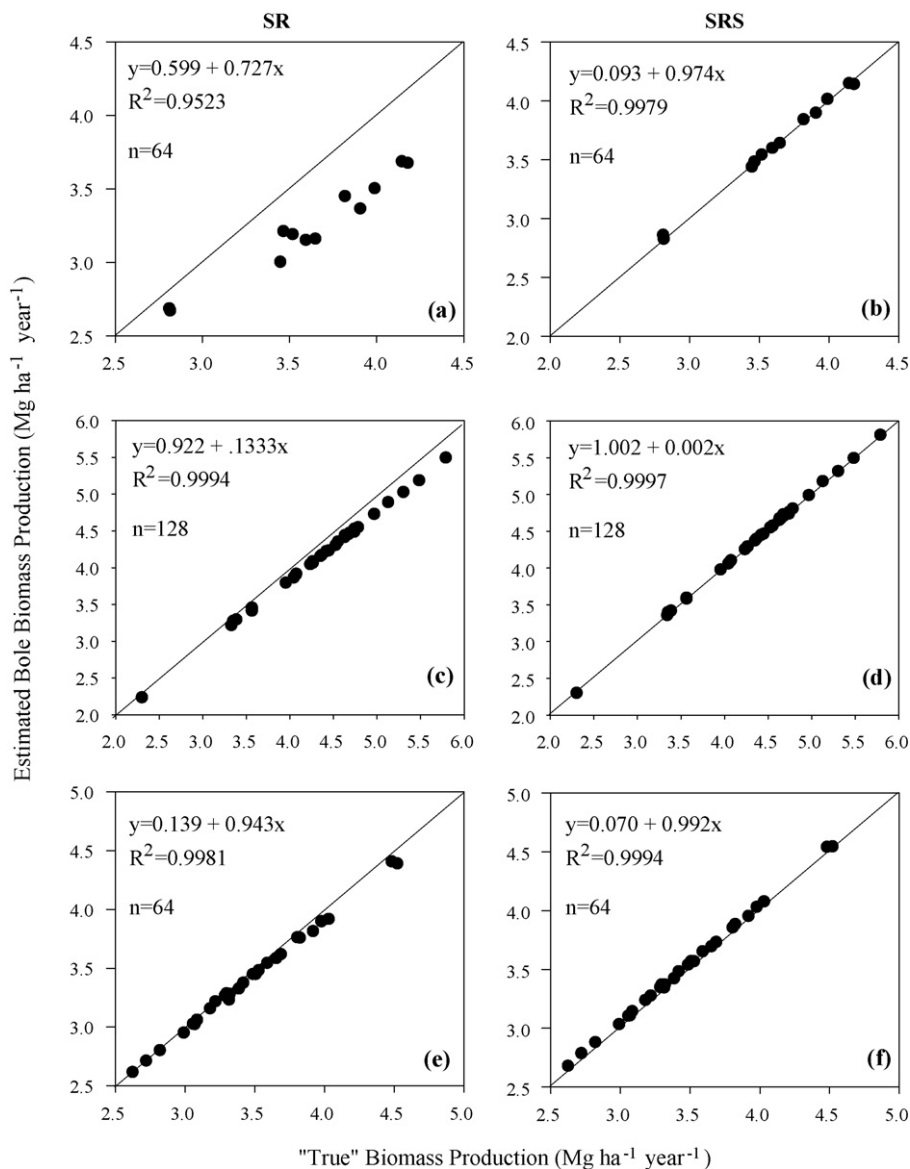
Fig. 3. Linear regressions of the estimated annual bole biomass production against "true" annual bole biomass production for both models, simple random (a, c and e) and stratified random (b, d and f). Left and right panels are paired by age (Y = young a and b, M=mature c and d, and OG=old-growth e and f). Diagonal lines represent a 1:1 relationship.

the highest sample size (90%), and 1–12% higher at the lowest sample sizes (10%). Across all sites, the average overestimation of individual years by the SRS model increased with site age. Annual BBP averaged across all years from the SRS model (Table 2) was biased by −0.0001, 0.025, and 0.042 Mg ha^{-1} year^{-1} for young, mature, and old-growth, respectively.

Linear regressions (Fig. 3b, d, and f) illustrate increased 1:1 relationships between estimated annual BBP and "true" annual BBP for all three sites compared to the SR model. Results from simultaneous F-tests indicate that either slopes were not equal to one or intercepts were not equal to zero, or both for the mature (p-value = 0.0009) and old-growth (p-value < 0.0001) sites.

The %CV of estimates (SRS) ranged from 3% to 4.5% across all three age classes as compared to %CV of the "true" annual

BBP of 12.5%, 16%, and 13.5% for the young, mature, and old-growth sites, respectively. The level of precision was within the bounds of inter-annual variability, indicating that estimates from the SRS model were also adequate to detect patterns of inter-annual variability (Table 2).

4. Discussion

The objective of this study was to evaluate whether two common sampling methodologies coupled with a simple statistical model can be used to accurately and precisely estimate annual bole biomass production and its inter-annual variability. Monte Carlo methods provided a tool to estimate the accuracy and precision of these estimates. Using this approach, we calculated the approximate sample sizes necessary to estimate stand-level annual BBP in long-term permanent plots

of varying age. Sub-sampling of trees with (SRS model) and without (SR model) stratification was simulated to model annual radial growth for non-sampled trees.

We determined that stratification by tree size was required to attain annual BBP estimates with desired accuracy and precision ($\pm 10\%$). The SR model did not accurately estimate annual BBP, and showed an increasing bias as annual BBP increased for all three age classes (Fig. 3). We attribute this bias mainly to a lack of normality in radial growth distributions. The bias caused an underestimation of the long-term average annual BBP and inter-annual variability. When stratification was applied to sampling and modeling radial growth, estimates of annual BBP were at least twice as accurate, with only a slight and consistent overestimation of 0.07 Mg ha^{-1} year^{-1} for the old-growth site.

Young and old-growth sites required similar sample sizes, whereas the mature site needed a sample size approximately twice that of the young and old-growth sites. The larger sample size required at the mature site could be due to higher variability of annual growth rates compared to the other two sites, or it is possible that in general this stage of forest succession has greater variability of growth among trees than either young or old-growth age classes. The lack of replication of age-classes in this analysis does not allow us to determine whether this site was typical of mature sites in the study area. Annual BBP estimates from this study (2.8–4.2, 3.3–5.8, and 2.6–4.5 Mg ha^{-1} year^{-1} for young, mature, and old-growth, respectively) are comparable to those found in previous studies. Grier and Logan (1977) reported tree bole biomass production of between 1.6 and 3.0 Mg ha^{-1} year^{-1} for old-growth sites in the area, but (Gholz, 1982) found rates of tree bole production for mature to old-growth sites more similar to ours (3.0–5.0 Mg ha^{-1} year^{-1}). Tree bole biomass accumulation (excluding mortality) estimates from Acker et al. (2002) in the same study area were very similar to ours (2.8–6.8, 4.0–5.0, and 2.2–2.3 Mg ha^{-1} year^{-1} for young, mature, and old-growth, respectively). Our estimates for the young site were slightly lower, but this difference could be attributed to our site being in an earlier stage of development than those of Acker et al. (2002). Overall, our estimates represent a wider range than found in previous studies, though this range in variability may be due to a longer study period (12, 32, and 32 years for young, mature, and old-growth, respectively).

The largest source of error when estimating tree biomass production has been shown to be the prediction of radial growth of non-sampled trees (Campbell et al., 2004). Some studies have sampled entire plots of trees (Graumlich et al., 1989) or taken a very large sub-sample within a site (440 trees; Grier and Logan, 1977) to remove this source of error. However, this approach is often not feasible for sampling large stands and/or for large numbers of plots across a larger study area. Different methods have been developed to deal with this error created by sub-sampling trees. For example, Jenkins et al. (2001) used linear regression models correlating diameter and radial growth to predict radial growth for non-sampled trees. Although this method is useful for making generalized estimates at the plot level, it does not predict uncertainty in estimates (i.e., it only predicts the average response). Moreover, this method may not maintain variability between plots because of site-to-site variation in diameter and radial growth relationships (Van Tuyl et al., 2005). Thus, without increased model complexity the value of this technique for examining temporal patterns between sites is limited. Campbell et al. (2004) and Van Tuyl et al. (2005) used a DBH quartile method, where mean radial growth for the trees in a quartile was assigned to the unmeasured trees in that quartile. We used a similar approach, but by using Monte Carlo methods and assigning radial growth randomly based on the mean and variance of a given quartile's distribution, we were able to estimate the uncertainty of our annual BBP estimates. By providing information about uncertainty, the Monte Carlo method allows the researcher to decide on sample size accordingly, and incorporate the inherent variability of radial growth into biomass estimates.

The method examined in this study can also be used to estimate annual production of trees lost to mortality in previous years. Although mortality can be a major flux (Harmon et al., 2004), it is often ignored in calculations of NPP (e.g., Graumlich et al., 1989; Campbell et al., 2004). However, underestimation of NPP occurs when mortality is not accounted for (Clark et al., 2001). For example, with an estimated biomass loss of 1% annually due to tree mortality (Franklin et al., 1987), estimates of annual NPP over a 20-year period could be underestimated by as much as 20%. Using the methods our analysis proposes, estimates and uncertainty due to tree mortality can be incorporated into calculations of annual NPP. Reconstruction of mortality-related NPP will be particularly useful for permanent plots where a record of mortality for individual trees exists, allowing estimation of NPP at the stand-level over longer periods of time than previous studies that have ignored this term. Other uncertainties involved in NPP estimation methods (e.g., uncertainty of biomass equations, measurement errors) can also be captured using methods similar to those described in this paper.

Although we have shown the method tested in this analysis can be a useful tool for predicting radial growth for non-sampled trees to estimate stand-level annual BBP, it may not be appropriate for all objectives (e.g., modeling individual tree growth patterns, forecasting annual productivity patterns). Given that this analysis involved time series, autocorrelation may need to be considered. Therefore, autoregressive models may hold the key to better prediction of individual tree growth, estimation of site-level annual BBP, and inter-annual variability. Different models or site/age-specific parameters may be necessary for estimating annual BBP of different age classes more accurately. For example, since the bias of estimates for the old-growth site appears consistent, it would be feasible to add a correction factor to the SRS model for older stands, or to subsequent estimates produced by this model. Also, our results indicate alterations in model structure and complexity may be needed to further reduce sample sizes (i.e., the addition of more predictive variables may improve accuracy and precision of model predictions). Increasing the complexity of the model however, may not lead to increased precision in estimates, but instead lead to greater uncertainty (Laurenroth et al., 2006).

Many studies (e.g., Law et al., 2001; Campbell et al., 2004; Harmon et al., 2004) have only measured a site(s) over 1–5 years to estimate annual NPP, and many times these estimates are averaged over measurement intervals of 2–5 years (e.g., Jenkins et al., 2001; Law et al., 2003; Harmon et al., 2004), rather than explicitly measuring NPP each year. Studies using chronosequence techniques (e.g., Acker et al., 2000, 2002; Law et al., 2001; Harmon et al., 2004) have investigated successional trends in biomass accumulation and NPP, but few have examined inter-annual variability (Knapp and Smith, 2001; Huxman et al., 2004) with data sets longer than 5 years. The limits of the current databases in both temporal and spatial extent have not given the opportunity to adequately estimate annual NPP and inter-annual variability, particularly in forests, over long-time periods (>10 years). An important objective of this analysis was to estimate annual BBP with precision great enough to allow detection of patterns of inter-annual variability. The error in our estimates was one-third to half that of the variation over time of annual BBP, indicated by lower %CV of estimates compared to inter-annual variability. Because annual BBP is a major component of NPP in forested ecosystems (accounting for 30–70% of total plant production), the approach examined in this analysis is the first step of a larger initiative examining patterns of inter-annual variability of NPP in permanent study plots.

5. Conclusions

Sub-sampling radial growth with stratification by tree size and application of a simple random model using Monte Carlo uncertainty analysis was shown to be an accurate ($\pm 10\%$) approach to estimating annual BBP for three different aged forest stands in the Pacific Northwest. A greater sample size (approximately 64–128 trees) than used in previous studies may be required to estimate annual tree BBP and tree NPP at the stand-level within 10% precision. Improvements to the model structure that address temporal autocorrelation of growth within trees may allow increased accuracy and precision, specifically at the individual tree level. Because the error of annual BBP estimates was smaller than the inter-annual variability of BBP, the method presented here can be used to examine inter-annual variability of NPP in forested ecosystems. Increasing our knowledge of this variability will improve our fundamental understanding of the potential responses of forests to changing climate and land use patterns.

Acknowledgements

Appendix 1

Allometric equations used to calculate total stem biomass (BST) in g for eight tree species, using diameter at breast height measurements (DBH). All equations are in the following form: $\ln(\text{BST}) = B_0 + B_1 \ln(\text{DBH})$.

Species	Site(s)	BIOPAK equation #	B_0	B_1
Pseudotsuga menziesii	RS07/RS32/WS06	256	4.660412	2.4247
Tsuga heterophylla	RS07/RS32/WS06	259	3.968674	2.5989
Thuja plicata	RS07/RS32/WS06	332	4.077376	2.4024
Taxus brevifolia	RS32	259	3.968674	2.5989
Calocedrus decurrens	RS32	386	2.112422	2.7818
Acer macrophyllum	WS06	35	−4.574	2.574
Prunus emarginata	WS06	43	3.1198	2.658
Castanopsis chrysophylla	WS06	43	3.1198	2.658

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