Comparing tree-ring and permanent plot estimates of aboveground net primary production in three eastern U.S. forests

Alex Dye,[1],† Audrey Barker Plotkin,[2] Daniel Bishop,[2] Neil Pederson,[2] Benjamin Poulter,[3] and Amy Hessl[1]

[1]Department of Geology and Geography, West Virginia University, Morgantown, West Virginia 26505 USA
[2]Harvard Forest, Harvard University, Petersham, Massachusetts 01366 USA
[3]Department of Ecology, Montana State University, Bozeman, Montana 59717 USA

Abstract.   Forests account for a large portion of sequestered carbon, much of which is stored as wood in trees. The rate of carbon accumulation in aboveground plant material, or aboveground net primary productivity (aNPP), quantifies annual to decadal variations in forest carbon sequestration. Permanent plots are often used to estimate aNPP but are usually not annually resolved and take many years to develop a long data set. Tree rings are a unique and infrequently used source for measuring aNPP, and benefit from fine spatial (individual trees) and temporal (annual) resolution. Because of this precision, tree rings are complementary to permanent plots and the suite of tools used to study forest productivity. Here we evaluate whether annual estimates of aNPP developed from tree rings approximate estimates derived from colocated permanent plots. We studied a lowland evergreen (Howland, Maine), mixed deciduous (Harvard Forest, Massachusetts), and mixed mesophytic (Fernow, West Virginia) forest in the eastern United States. Permanent plots at the sites cover an area of 2–3 ha, and we use these areas as benchmarks indicative of the forest stand. We simulate random draws of permanent plot subsets to describe the distribution of aNPP estimates given a sampling area size equivalent to the tree-ring plots. Though mean tree-ring aNPP underestimates permanent plot aNPP slightly at Howland and Fernow and overestimates at Harvard Forest when compared with the entire permanent plot, it is within the 95% confidence interval of the random draws of equal-sized sampling area at all sites. To investigate whether tree-ring aNPP can be upscaled to the stand, we conducted a second random draw of permanent plot subsets simulating a twofold increase in sampling area. aNPP estimates from this distribution were not significantly different from results of the initial sampling area, though variance decreased as sampling area approaches stand area. Despite several concerns to consider when using tree rings to reconstruct aNPP (e.g., upscaling, allometric, and sampling uncertainties), the benefits are apparent, and we call for the continued application of tree rings in carbon cycle studies across a broader range of species diversity, productivity, and disturbance histories to fully develop this potential.

Key words: biomass; carbon cycle; dendrochronology; eastern United States; net primary productivity; permanent plots.

† **E-mail:** aldye@mix.wvu.edu

Introduction

Forests account for a large portion (up to 80%) of total sequestered live terrestrial biomass, and are essential to understanding the global carbon cycle (Dixon et al. 1994, Pan et al. 2011). Temperate forests in the Northern Hemisphere, especially those in eastern North America, comprise some

of the largest and most active terrestrial global carbon sinks (Pacala et al. 2001, Goodale et al. 2002). However, the large, dynamic interannual variability in the terrestrial carbon sink is poorly understood and requires better quantification if this sink is to be managed.

Interannual changes in forest productivity are typically quantified using a variety of methods, including biometric (manual measurement of tree growth), eddy covariance measurements of the influx and outflux of CO_2 (Barford et al. 2001, Baldocchi 2003, Hollinger et al. 2004), and remote sensing (Running et al. 2004, Ollinger et al. 2007). Attempts at incorporating these data into ecosystem models to estimate productivity over longer timescales have achieved varying results (Friedlingstein et al. 2010, Jones et al. 2013), and a more detailed understanding of forest productivity is needed to improve forecasts of carbon dynamics under climate change and managed terrestrial sequestration.

Net primary productivity (NPP) is defined as the biomass increment of woody and herbaceous plants in terrestrial ecosystems and is the difference between total photosynthetic uptake, or gross primary productivity, and losses from autotrophic respiration (Chapin et al. 2006). Total NPP in forests can be quantified by summing the carbon allocated to all components of the plant including sapwood in stems, branches, fine roots, and live foliage. Measurement of each of these carbon fluxes requires different techniques (see Clark et al. 2001 for a comprehensive review). Aboveground net primary productivity (aNPP) is important in forests because of the long-term storage capacity of carbon gained by wood (preventing carbon release to the atmosphere) and commercial interest in forest woody carbon stocks (Harmon et al. 1990, Fahey et al. 2009).

Biometric methods, such as permanent plots and tree rings, quantify incremental tree growth over time to estimate aNPP. These methods can develop aNPP records over relatively long timescales (decades), and robust techniques and applications have been described for permanent remeasurement plots (Siccama et al. 2007, Schuster et al. 2008, Xu et al. 2012, Fahey et al. 2013, Eisen and Barker Plotkin 2015) and for tree rings (Graumlich et al. 1989, Davis et al. 2009, Xu et al. 2012, Babst et al. 2013b, Babst et al. 2014). The biomass of individual trees can be calculated with species-specific allometric equations relating stem diameter to aboveground dry weight of wood and aNPP calculated as the change in biomass over a time interval (where carbon content is typically 50% of biomass). The main attraction of using tree rings or permanent plots to measure biomass increment is the ability to track aNPP of individual trees, advantageous for the study of aNPP variability at the local scale.

In permanent plots, all trees above a certain diameter threshold are remeasured periodically and aNPP defined as the change in biomass between measurements. Permanent plots provide an excellent record of productivity over time because they track growth and mortality of individual trees. No other method is capable of precisely quantifying biomass lost to mortality. However, permanent plots require decades of intensive labor to obtain meaningful results and rarely capture the interannual dynamics of aNPP. Error in permanent plot studies can stem from discrepancies in measurements between field workers, differences in the season measurements were taken, non-growth-related expansion or contraction of bark, and human error measuring tree diameters (McRoberts et al. 1994, Holdaway et al. 2014).

Tree rings serve as reliable indicators of biomass increment (Bouriaud et al. 2005) and are recognized as a valid source for estimating aNPP (Clark et al. 2001, Kloeppel et al. 2007), but they have only rarely been used as a measure of biomass accumulation (Babst et al. 2014, Hember et al. 2015). Tree rings have the potential to preserve decadal to centennial scale variability in aNPP, but their accuracy needs to be demonstrated across a range of sites with different species composition, rates of productivity, and disturbance histories.

Tree rings minimize many challenges in quantifying productivity by providing very fine temporal (annual) and spatial (the individual tree) resolution with only a single sampling effort. However, use of tree rings includes a loss of information about trees that died previously and could not be sampled (Foster et al. 2014) and allometric uncertainties in scaling ring width to total biomass increment (Dietze et al. 2008, Alexander et al. 2015), an uncertainty that affects remeasurement plots as well. In addition, tree-ring collections developed for specific studies involving climate reconstructions, stand dynamics, stream

flow, or disturbance history, for example, rarely include a complete census of trees in a fixed-area plot, which is critical for developing stand-level productivity estimates on a per area unit scale (Babst et al. 2013*a*, Nehrbass-Ahles et al. 2014).

Both tree-ring and permanent plot estimates of aNPP aim to develop estimates that describe the whole stand in addition to individual trees or sampling plots because this vastly expands our inferential capabilities. However, upscaling aNPP from the plot-level can be problematic, especially in forests with considerable species and structural heterogeneity (Weins 1989). Growth rates and allocation percentages of carbon to aboveground plant components can vary by species and tree size, and failure to include a representative selection of the species and structural diversity present in a forest has potential to bias estimates of stand-level aNPP.

Permanent plots are an established standard method for estimating aNPP and can be further improved with the annual resolution that tree rings provide (Metsaranta and Leiffers 2009). However, extensive comparisons of tree-ring and permanent plot estimates of aboveground productivity are generally lacking in the literature, and a more complete set of studies across varied forest types combining these two methods is needed to ask the fine-scale ecological questions that can only be addressed using these biometric approaches. Biondi (1999) analyzed tree-ring chronologies in the Western United States with growth rates of trees in U.S. Forest Service inventory plots, but did not explore biomass increment. A recent study in Europe used a combination of tree-ring and permanent plot basal area increment to study climate response over the length of forest measurement intervals, but did not perform an explicit comparison or quantify aNPP (Rohner et al. 2016), and Klesse et al. (2016) conducted one of the first and only integrations of tree-ring and permanent plot measurement for the express purpose of improving estimates of aboveground biomass increment in a Scots pine dry valley forest. While Klesse et al. (2016) observed strong agreement between both methods, they studied a nearly monospecific forest in Switzerland, and work on forests with alternative species composition, ages, and stand structure will add to their progress.

In this study, we compare field estimates of aNPP derived from tree rings with estimates from colocated permanent plots for a temperate coniferous, mixed deciduous, and mixed mesophytic forest in the eastern United States. By analyzing tree-ring aNPP in concert with another well-established biometric method, we develop a basis for how much confidence we can place in tree-ring estimates and the types of inferences they allow us to make. We evaluate different configurations of our data set to investigate how area sampled and variability in species and structural diversity influence the comparison and assess to what extent we can scale up aNPP from a small collection of plots. We use these analyses to inform future sampling campaigns and call attention to the benefits of including both tree rings and permanent plots in carbon sequestration research.

METHODS

Study areas

We included three sites representing differing forest types of the eastern United States in this analysis (Fig. 1). Howland Research Forest is a lowland coniferous forest in central Maine dominated by eastern hemlock (*Tsuga canadensis* L.) and red spruce (*Picea rubens* Sarg.) with subdominates red maple (*Acer rubrum* L.), eastern white pine (*Pinus strobus* L.), northern white cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* L.), and yellow birch (*Betula allegheniensis* Britton). Harvard Forest is a mixed deciduous forest in central Massachusetts dominated by red oak (*Quercus rubra* L.) and red maple, with subdominates American beech (*Fagus grandifolia* Ehrh), eastern hemlock, eastern white pine, and yellow birch. Fernow Experimental Forest is a mixed mesophytic forest located in the Allegheny Mountains of West Virginia composed predominately of red oak, chestnut oak (*Quercus montana* Willd.), scarlet oak (*Quercus coccinea* Menchh.), American beech, red maple, sugar maple (*Acer saccharum* Marsh.), black cherry (*Prunus serotina* Ehrh.), and American basswood (*Tilia americana* L.). We chose these sites for proximity of tree-ring data and ongoing permanent plots, and each differ in species composition, forest age, productivity, and data availability (Table 1).

Tree-ring aNPP estimates

At Howland and Harvard forests, we established nested circular plots with a 20-m radius,
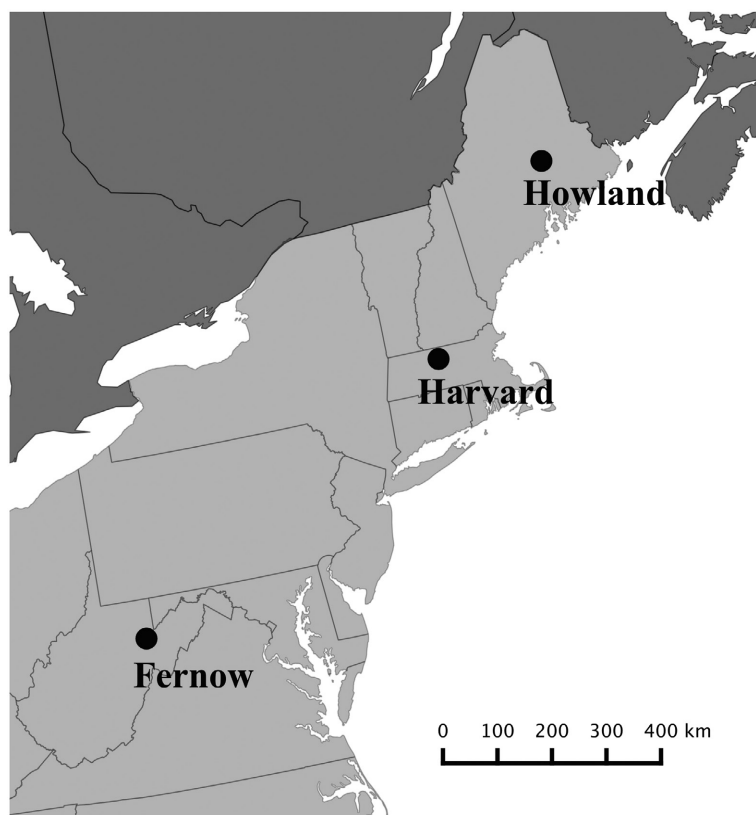
Fig. 1. Map of three study sites included in this analysis: Howland Research Forest, Harvard Forest, and Fernow Experimental Forest.

coring all trees ≥10 cm diameter at breast height (dbh) within a 13-m radius and all trees ≥20 cm dbh between 13 and 20 m. The dominant trees in a forest may account for up to 95% of total aboveground biomass (Kloeppel et al. 2007), but are rare, requiring a larger sample area. This design ensures adequate sampling of larger trees when time and resources limit the feasibility of

sampling all trees in multiple 20 m radius plots. To account for growth differences caused by tree asymmetry, we collected two cores from each tree. We sampled three plots at Howland. At the Harvard Forest, we deliberately placed three tree-ring plots within the permanent plot study area (the "Lyford plots"). Because of concerns about long-term monitoring, we were unable to place

Table 1. Summary characteristics of the three study sites.

Site, dominant forest type, and age	Method	Timescale†	Reference
Howland: *P. rubens, T. canadensis* Approx. age: 140 yr	Tree rings	1989–2013	This paper
	Permanent plots	1989, 1998, 2009	J. Lee (*personal communication*)
Harvard: *Q. rubra, A. rubrum* Approx. age: 115 yr	Tree rings (Lyford)	1969–2012	This paper
	Tree rings (EMS)	1969–2012	This paper
	Permanent plots	1969, 1975, 1991, 2001, 2011	HF Data Archive HF032
Fernow: *Q. rubra, Q. montana, A. rubrum, A. saccharum, P. serotina* Age: 100 yr	Tree rings	1979–2002	Davis et al. (2009)
	Permanent plots	1979, 1983, 1989, 1994, 1999, 2009	F. Wood (*personal communication*)

† Range of annual data (tree rings) or years when measurements occurred (permanent plots).

plots inside the permanent plot boundaries at other sites. Ideally, the aNPP estimates are meant to be indicative of the entire forest, not just the plot, and this locational offset allows us to assess this assumption. Additionally, two tree-ring plots (the "EMS plots") were established outside the Harvard Forest permanent plot study area near the EMS (Environmental Monitoring Site) eddy covariance tower. Tree cores at Fernow were collected in 2002 for a study comparing forest productivity with management strategy (Davis et al. 2009). Two cores were removed from all trees ≥10 cm dbh in six 10 m radius plots.

We dried, mounted, and sanded cores according to standard dendrochronological procedure (Stokes and Smiley 1968). To ensure annual dating, we visually cross-dated ring widths using the skeleton plotting method. We measured all rings to 0.001 mm accuracy using a measuring stand and binocular microscope and statistically confirmed cross-dating using COFECHA (Holmes 1983). We averaged ring widths from all cores per tree and scaled measurements from radius to diameter.

We used regional, species-specific allometric equations to calculate aboveground biomass increment of each living tree (Appendix S1). Because developing site-specific equations is beyond the scope of this study, we selected equations from published studies that most closely matched the relevant diameter range, forest type, and species. We used equations either of the form $M = a \times D^b$ or $\ln(M) = a + b \times \ln(D)$, where M is total aboveground dry weight of the tree (stem, branches, foliage) in kg, D is stem diameter in cm, and a and b are species-specific coefficients. To calculate annual biomass increment of each tree, we subtracted previous ring increments from the current diameter and reapplied allometric equations on the reconstructed diameter (Davis et al. 2009). We define aNPP as the per hectare sum of annual biomass increment of all trees in a plot. We assume carbon content to be 50% of dry weight, per standard conventions (Fahey et al. 2005). For the nested plots (Howland and Harvard), a plot total was defined as the per hectare sum of the inner plot (all trees ≥10 cm and <20 cm) and the outer nest (all trees ≥20). A site average was defined as the average of all plots, and interplot variability represented as the range of estimates of the three plots. All calculations

and data management were performed in R (R Development Core Team 2015).

Permanent plot productivity estimates

At Howland, a 3-ha permanent plot (with 48 subplots, each 625 m^2) was established in 1989, and all trees >4 cm dbh were measured in 1998, 2002, and 2010 (J. Lee, *personal communication*). The Lyford permanent plot at Harvard Forest was established by Walter Lyford for long-term forest study in 1969. Covering a 2.88-ha area, the single, large plot was subdivided into 32 blocks, each 930 m^2. Measurements of all trees >5 cm dbh were taken in 1975, 1991, 2001, and 2011 (HF Data Archive HF032, Eisen and Barker Plotkin 2015). Unlike at Howland and Harvard, the Fernow permanent plots are not spatially contiguous. Ten permanent plots, each 0.5 acres, were established in the WS4 section of Fernow in 1979. Measurements were taken on all trees >5 cm dbh in 1983, 1989, 1994, 1999, and 2009 (F. Wood, *personal communication*).

Because the minimum diameter requirement for sampling varied between the three forests (4 cm at Howland, 5 cm at Lyford, and 5 cm at Fernow), we subsetted all permanent plot data sets to include only trees that were at least 10 cm dbh at any time during the census period to provide consistency with the tree-ring data. Measurements of trees that grew into this size class from one census to the next were also included to account for ingrowth. Trees that died in between time steps were attributed zero growth for all subsequent intervals. For context, we also provide the full permanent plot data sets without subsetting to a minimum diameter (Appendix S2).

For instances when individual trees were missing a measurement entry for a given year (measurement error), an interpolated value was calculated using the previous and subsequent measurement for that tree. Missing values occurring in the final census, preventing interpolation, were replaced with the average absolute increment for other trees of the same species.

We calculated aboveground biomass as the biomass of living trees present at each census year and aNPP as the difference in aboveground biomass of surviving trees between census points divided by the number of intervening years (Clark et al. 2001). We applied the same allometric equations used for tree-ring aNPP calculations.

Statistical comparisons

Total area sampled varied between permanent plots and tree-ring plots. We compared tree-ring aNPP estimates with permanent plot estimates from approximately equal-sized sampling areas to show biases associated with sample size and display the extent that our tree-ring sampling area is representative of an equivalent sampling area from the permanent plots. Total area sampled for tree rings was 3768 m^2 at Howland and the Harvard Lyford plots and 1884 m^2 at Fernow. Six census subplots (3750 m^2) at Howland, four census subplots (3721 m^2) at Harvard, and one census subplot (2023 m^2) at Fernow approximately equal the total area cored at their respective sites. From the Howland and Harvard permanent plot data, we drew 10,000 random samples of six and four plots, respectively, and recalculated aNPP to construct a distribution of possible estimates given a specific sampling size. The small number of subplots at Fernow did not allow for sufficient random sampling, and aNPP variability was described as the distribution of the 10 individual subplots.

We evaluated differences between the tree-ring and permanent plot estimates with a Mann–Whitney–Wilcoxon (MWW) test, using the wilcox.test function in R (R Core Team 2015). MWW is a nonparametric test that tests the null hypothesis that both tree-ring and permanent plot aNPP estimates come from the same distribution. We used a nonparametric test because it is difficult to assume normality with so few data points. Additionally, we use the MWW location parameter to quantify the extent one distribution over- or underestimates another distribution and examine consistent biases between tree rings and permanent plots.

To investigate how well the tree level data can be scaled up to the stand level, we conducted a second round of random resampling from the Howland and the Harvard permanent plots hypothetically assuming the size of each tree-ring plot was increased to a 30-m radius, more than doubling the area of forest sampled. This sampling design equates to approximately 13 subplots from the Howland permanent plot and nine subplots from the Harvard permanent plot. At Fernow, where only 10 permanent subplots are available, we repeatedly drew combinations of two subplots, approximately doubling the forest area sampled for tree rings. We conducted another MWW test at each site comparing these new simulated distributions with our original permanent plot resamples.

RESULTS

aNPP reconstructions

To develop estimates of annual aNPP from tree rings, we measured two increment cores per stem for 266 live trees at Howland, 287 trees at Harvard Forest (136 at Lyford plots, 151 at EMS plots), and 132 trees at Fernow. Permanent plots resulted in at least one measurement of over 7000 trees at Howland, 6000 trees at Harvard Forest, and 1500 trees at Fernow. We present a more detailed plot inventory describing biomass distributions by size and species for each of the tree-ring and permanent plots in Appendix S3.

The range of individual tree-ring plot estimates for each year (Fig. 2) is minimal at Howland (maximum range of 0.39 Mg C/ha in 2006), Lyford (maximum range 0.79 Mg C/ha in 1971), and EMS (maximum range 0.53 Mg C/ha in 2010), but is wide at Fernow (maximum range of 5.4 Mg C/ha in 2001). At Fernow, an analysis focused on only one of these plots could produce aNPP estimates anywhere from 1 to over 6 Mg C/ha in a given year. At Harvard Forest, where tree-ring plots were installed within (Lyford plots) and separate (EMS plots) from the permanent plots, both annual tree-ring aNPP series correlate significantly over the period 1969–2012 (Pearson's $r = 0.74$, $P < 0.001$).

Comparisons with permanent plot aNPP

For all census periods and sites, tree-ring aNPP estimates are within the 95% confidence intervals of possible estimates from 10,000 resamples of equal-sized sampling areas (Fig. 2). There is considerable variability in permanent plot aNPP draws for each time interval, ranging from a low standard deviation of 0.20 Mg·ha^{-1}·yr^{-1} over the 1975–1991 interval at Harvard Forest to a 0.41 Mg·ha^{-1}·yr^{-1} standard deviation over the 2002–2010 interval at Howland. Overall, variability in the resampled distribution is lowest for all intervals at the Harvard Forest permanent plots.

The MWW test of equality for tree-ring and permanent plot aNPP when the entire permanent plot data set is considered is significantly different ($P > 0.05$) for Harvard (both Lyford and
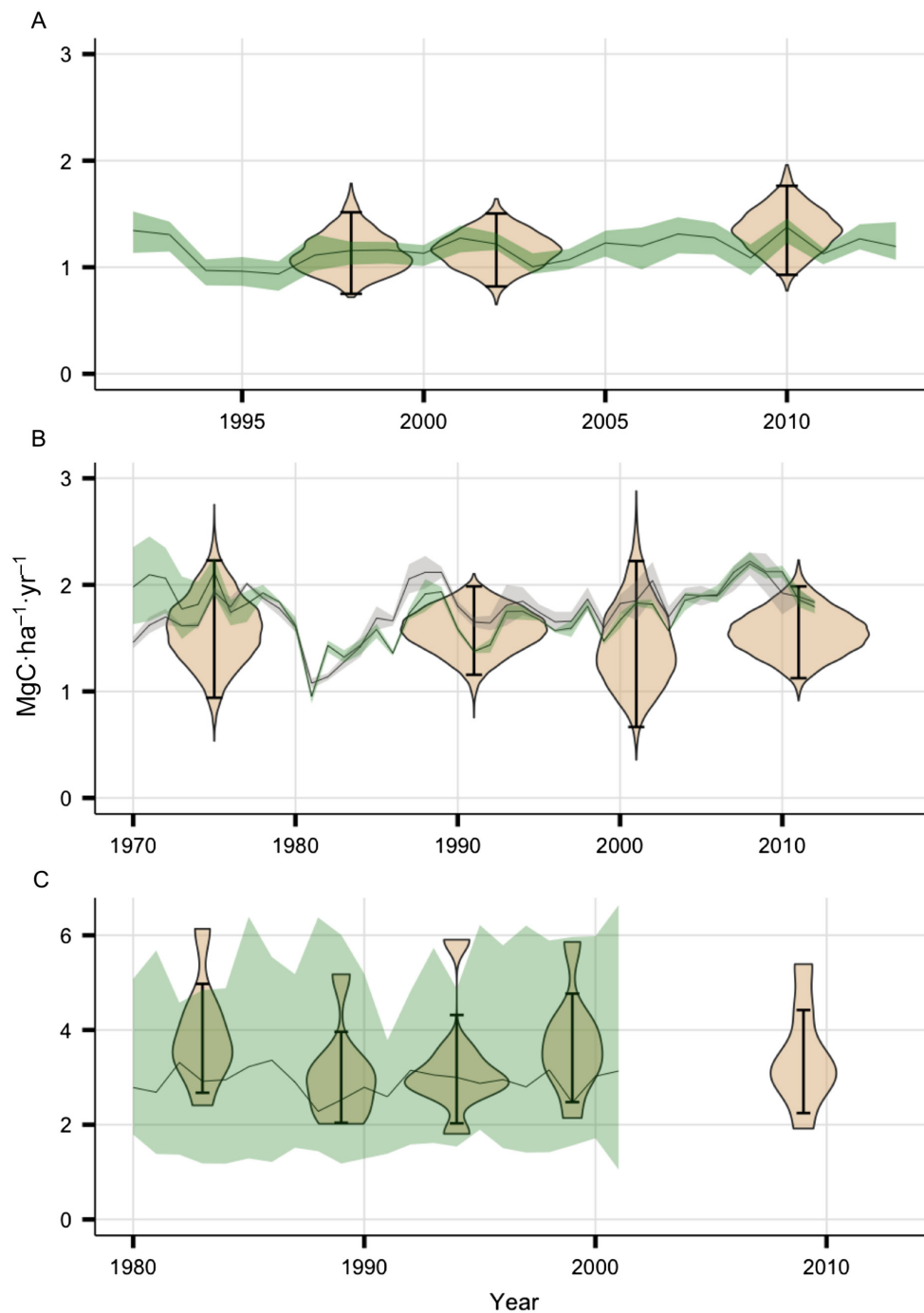
Fig. 2. Graphical comparisons of tree-ring aboveground net primary productivity (aNPP) versus permanent plots at (A) Howland Research Forest, (B) the Harvard Forest, and (C) Fernow Experimental Forest. Green ribbons represent the range of aNPP across all tree-ring sampling plots, with the mean marked by the black line. At Harvard, gray ribbons represent the EMS tree-ring plots and green ribbons the Lyford tree-ring plots. Beige violin plots show the distribution of aNPP estimates from 10,000 random subsets of the permanent plot data equal to the area cored. At Fernow, violin plots represent the distribution of aNPP from all 10 subplots. Error bars denote 95% confidence intervals for the resampled distributions.

Table 2. Results of the Mann–Whitney–Wilcoxon test of equality of tree-ring and permanent plot aboveground net primary productivity.

Site	P	Location parameter (95% CI)†
Howland	0.51	0.15 (−0.3, 0.18)
Harvard Lyford	0.03*	−0.29 (−0.51, −0.01)
Harvard EMS	0.03*	−0.19 (−0.52, −0.06)
Fernow	0.03*	0.59 (0.12, 1.04)
All	0.37	−0.11 (−0.42, 0.39)

* Significant at <0.05 level.
† Tests were conducted as permanent plots against tree rings, so positive values indicate overestimation by permanent plots and negative values overestimation by tree rings.

EMS) and Fernow (Table 2). Results at Howland are not significantly different, suggesting the tree-ring and permanent plot aNPP populations are equivalent. The test is also not significant when all sites are grouped together. Location parameters from the MWW test show that tree-ring aNPP is underestimating permanent plot aNPP at Howland and Fernow and overestimating at Harvard (Table 2, Fig. 3). Tree rings slightly overestimate permanent plots when all sites are grouped together. Interannual variability in aNPP (assessed as the range of all annual aNPP values over the study period) is greater for
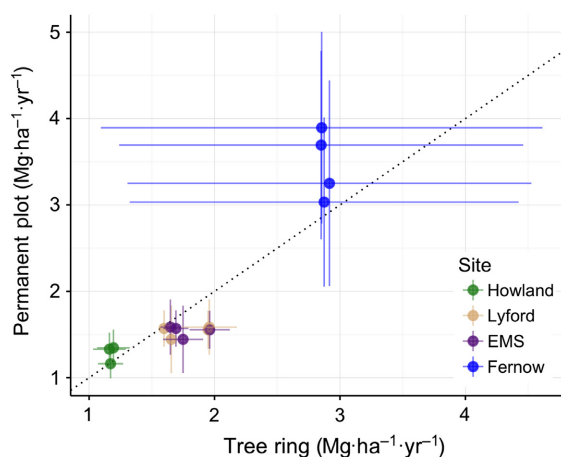

Fig. 3. Tree-ring aboveground net primary productivity (aNPP) is plotted against permanent plot aNPP for all remeasurement intervals at the three sites. Error bars are ±1 SE above the mean for tree rings (horizontal) and permanent plots (vertical). The black dashed line represents the one-to-one relationship. Points above this line indicate underestimation by tree rings and points below indicate overestimation by tree rings.
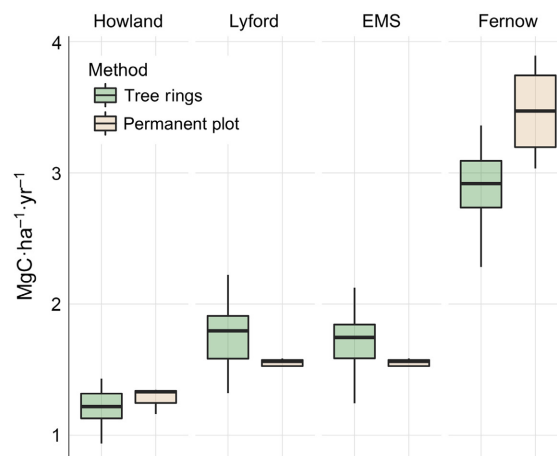

Fig. 4. Boxplots showing the distribution of annual tree-ring aboveground net primary productivity (aNPP) estimates across all years overlapping with permanent plots. Beige boxplots show the distribution of aNPP for all permanent plot intervals. Tree rings from the Harvard Lyford and EMS tree-ring plots are both compared with Lyford permanent plots.

the tree-ring estimates than for permanent plots at all sites (Fig. 4).

Upscaling

In our upscaling analysis, the MWW test of equality between the distribution of permanent plot aNPP resamples of equal forest area to the tree-ring plots and the distribution of resamples simulating a hypothetical larger tree-ring sampling area is not significantly different for Howland ($P = 0.05$), Harvard ($P = 0.18$), or Fernow (0.65), indicating that there is no difference in aNPP estimates when the sampling area is increased in this manner. However, increasing the area of forest sampled tightens the variability around the mean (Fig. 5). Standard deviation decreases from 0.21 to 0.15 at Howland, 0.30 to 0.19 at Harvard, and 1.08 to 0.61 at Fernow.

DISCUSSION

Many attempts at using dendrochronology to retroactively calculate aNPP are beset with numerous biases inherent in the sampling design (Bowman et al. 2013, Nehrbass-Ahles et al. 2014). Some common problems include the "modern sampling bias," in which only trees alive at the
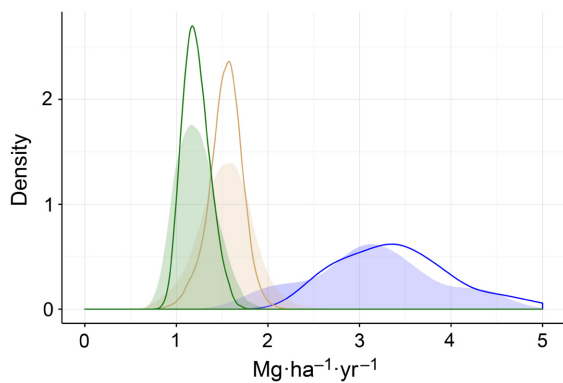
Fig. 5. The distribution of aboveground net primary productivity estimates from permanent plots resulting from 10,000 random combinations of subplots equaling the area sampled by tree rings (solid fill) is shown against the distribution of estimates from permanent plot draws simulating a larger sampling area (transparent fill). Green curves are Howland, beige curves Harvard, and blue curves Fernow.

time of sampling are analyzed (Cherubini et al. 1998, Briffa and Melvin 2011), the "slow-grower bias," which assumes older trees have slower growing rings (Bigler and Veblen 2009, Brienen et al. 2012), the "big-tree selection bias," in which only the largest, most dominant trees are sampled (Brienen et al. 2012), the "predeath suppression bias," in which a growth decrease is observed due to the inclusion of old, slow-growing trees in the analysis (Pederson 1998, Wyckoff and Clark 2002), and the "fading record bias," in which an apparent decrease in growth is seen back in time due to trees that are not included because they died before the time of sampling (Foster et al. 2014).

Because permanent remeasurement plots track growth as it occurs, these data are less susceptible to these biases. Recognizing the presence of these biases in tree-ring aNPP reconstructions, we attempted to control for them in three ways. (1) We sampled all trees over a specified dbh threshold within our delineated plots, and follow a "fixed-plot" design, shown to be one of the most effective sampling methods for obtaining aNPP estimates (Babst et al. 2013a). This minimizes biases associated with only including the oldest, most dominant trees in a stand. However, we are still missing growth information on trees that died during the study period. (2) We only included aNPP estimates from the previous

30–40 yr. Many of these biases increase in magnitude further into the past, but our aNPP reconstructions are not obviously affected over this short time period; that is, we observe no increase in the difference between tree rings and permanent plot data going back in time. However, when increasing the study extent to >60 yr before present, tree-ring aNPP estimates plummet unrealistically (Appendix S4). (3) By calculating aNPP as an areal mass sum (Mg C/ha), we obtain a plot-level aNPP measure, minimizing abnormal contributions of individual trees to growth in every year.

While the potential for tree rings to supplement permanent plots has been suggested previously (Metsaranta and Leiffers 2009, Rohner et al. 2016), explicit comparisons between the methods have only been conducted in a Scots pine stand in the Swiss Alps (Klesse et al. 2016) and a ponderosa pine forest in the American southwest (Biondi 1999). Klesse et al. (2016) documented tree-ring aNPP consistent to within <0.1 $MgC \cdot ha^{-1} \cdot yr^{-1}$ of colocated permanent plot aNPP over a 14-yr period, which is comparable to our results at Howland but more constrained than we observed at Harvard or Fernow. However, their stand was nearly 98% monospecific, and our current analysis is the first to present a comparison for the dense, diverse forests characteristic of the eastern United States.

We have shown that tree-ring aNPP estimates are within the 95% confidence interval of the distribution of reassembled equal-area samples of permanent plots (Fig. 2). Because of this agreement, we claim that both tree-ring and permanent plots are producing estimates that are within a reasonable proximity. However, tree-ring aNPP tends to overestimate permanent plot aNPP at Harvard and Fernow and underestimate at Howland when a comparison with the whole permanent plot data set is considered (Fig. 3). Because the permanent plots at our sites cover 2–3 ha of forest, we consider these aNPP estimates to be generally representative of the stand, with our tree-ring aNPP overestimating stand-level aNPP at Harvard and Fernow and underestimating at Howland.

Understanding the extent that plot-based aNPP estimates can be upscaled to the stand or ecosystem scale is another area of inquiry, and further upscaling beyond the stand is problematic due to potential larger-scale variations that cannot be addressed using our localized data sets (Fahey

et al. 2015). We addressed the upscaling problem in our data by comparing distributions of permanent plot aNPP estimates calculated from two different areal extents, one equal to the area sampled in our tree-ring plots and one simulating an approximately twofold increase in tree-ring sampling area (Fig. 5). These two distributions were not significantly different for any of our three sites, indicating that increasing the forest area sampled in this manner does not provide estimates that are significantly better. But, the spread of potential aNPP estimates does decrease, which would continue to occur until a sampling area equivalent to the permanent plots is achieved, and we can expect the tree-ring aNPP estimates to move closer to the permanent plot (stand-level) aNPP estimates as we increase our sampling area.

Fully addressing the problem of upscaling past the stand level will likely involve integrating multiple data sources developed at various scales, including remote sensing, eddy covariance, and modeling in addition to tree rings and permanent plots. Our present comparison of tree-ring and permanent plot aNPP adds to a growing body of literature working toward this goal (e.g., Rocha et al. 2006, Bunn et al. 2013, Babst et al. 2013b, Girardin et al. 2014, Klesse et al. 2016). Additionally, upscaling aNPP estimates for forests of high heterogeneity may be even more difficult because a particular sampling plot will not necessarily include all representative species or habitat types (e.g., ridges, valleys, riparian areas). Both our tree-ring and permanent plot aNPP estimates at Fernow, which has high species diversity and contrasting topography, have a considerably wide range between individual sampling plots (Fig. 2). This range is less pronounced at both Howland and Harvard, which have more homogeneity in species and topography, although all three sites exhibit higher heterogeneity than sites where a similar comparison has been previously conducted (Biondi 1999, Klesse et al. 2016).

Absolutely resolving the issue of a mismatch in sampling area between both methods would require tree-ring aNPP reconstructions from every tree within the permanent plots or every tree within an equivalent-sized area, which is not a data set we have developed at this time. When colocated permanent plot data are available, however, an approach similar to our equal-area resample can help contextualize tree-ring aNPP estimates from a particular sampling area. The ability to contextualize tree-ring aNPP estimates with permanent plots is becoming increasingly possible, as sites that have prioritized colocation of long-term ecological data sets, including those in this study, are developing longer and longer growth records from permanent plots (e.g., Woods 2007, Anderson-Texeira et al. 2015).

Another issue associated with using tree growth increment to calculate aNPP is the uncertainty associated with using species-specific allometric equations to translate diameter growth to aboveground carbon gain (Fatemi et al. 2011, Babst et al. 2014, Temesgen et al. 2015). Site-specific allometric equations are rarely available, and researchers must use their judgment to select a set of equations published for other sites. For this study, we carefully selected the best equations to use based on criteria of geographic proximity to study sites and the size distribution and number of trees from which the equations were developed. Despite efforts to apply the best equations given our criteria, it is still impossible to absolutely validate their accuracy without having explicit allometric information from each site (Arthur et al. 2001). Constraining the uncertainties surrounding allometric equations is an urgent area of research that is actively being addressed (Dietze et al. 2008, Nickless et al. 2011, Zell et al. 2014, Alexander et al. 2015). However, in our work, as we used the same equations for all trees of the same species at each site for both methods, any uncertainty related to allometric equations effect both tree-ring and permanent plot aNPP equally and we do not explicitly pursue this uncertainty.

Despite some of the challenges with using tree rings, they are a unique data source for developing high-resolution reconstructions of forest productivity and possess the potential to improve the overall detail of growth records when used in concert with colocated permanent plots. Differences in the strength of the agreement and range of tree-ring and permanent plot aNPP estimates between our three study sites suggest that the confidence with which we can equate both aNPP estimates, as well as the ability to upscale to the stand level and beyond, may vary by forest type. Therefore, future studies in this vein should focus on a variety of additional forest types, including those with a range of high species diversity, compositions, ages, and management strategies.

Conclusions

Permanent plots are the ecological standard for tracking productivity of forest stands over time and are an ideal data set for contextualizing aNPP estimates developed from tree-ring plots. Comparisons such as our study are a necessary step toward developing more complete, multimethod data sets. As many of the strengths and weaknesses of each method are complementary, combining data sets can improve detail and applicability of long-term measurements. As permanent plot data become available over more years at more sites, we encourage continued research combining colocated tree-ring records to further develop what we have presented here for three eastern U.S. forest sites. Further, these permanent plots are critical for understanding the role of forest management in terrestrial carbon sequestration and should be maintained and supported. Combining these two data sources provides opportunities for modeling of spatial, temporal, and ecological dynamics of annual aNPP at a variety of scales. Additionally, we promote the continued use of tree rings to estimate aNPP for forests that differ in species composition, age, rates of productivity, and disturbance histories. Tree rings are still a relatively rarely used method for estimating aNPP, and additional comparisons with permanent plots in high diversity sites will help reduce the uncertainties with using tree rings in carbon cycle research.

Acknowledgments

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Supporting Information