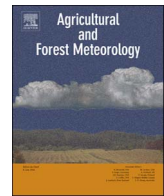




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Linking annual tree growth with eddy-flux measures of net ecosystem productivity across twenty years of observation in a mixed conifer forest

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ABSTRACT

Eddy covariance methodologies have greatly improved our understanding of the forest carbon cycle, including controls over year-to-year variability in productivity (measured as net ecosystem productivity, NEP, where NEP is the difference between the mass of carbon fixed by photosynthesis and that lost by ecosystem respiration). However, establishing and maintaining eddy covariance towers requires sizeable financial and logistical investments. Tree-ring methods, which can produce annual estimates of tree biomass increment from individual trees, provide an alternative approach for assessing forest productivity. Attempts to link these measures of productivity (i.e., NEP and tree biomass increment) have produced inconsistent results, in part because NEP time series are typically too short to provide robust comparisons. We here use a relatively long (20-year) NEP time series together with annual tree biomass increment (derived from tree-ring data) from the same site to determine to what extent the two productivity measures relate to each other. We conducted this study at the Howland Research Forest, central Maine USA, which supports a mature, mixed-species conifer forest. We expressed stand-level tree biomass increment on a per-area basis, which allowed direct comparisons with NEP data. Our results revealed a strong relationship between tree biomass increment and annual NEP measurements when the latter are summarized from previous-year fall to current-year fall, a marked improvement over more typical calendar-year summaries. Further, our results suggest tree biomass increment lagged one year behind NEP (i.e., assimilated carbon was not allocated to wood formation until the following year) for roughly the first half of the time-series, but later became synchronized with current-year NEP. This shift to synchrony may reflect a change in stand-level carbon allocation and growth dynamics. The apparent shift in carbon allocation from storage into current-year wood formation is most evident in two recent years with above-average spring temperatures. Although our results demonstrate a link between annual tree biomass increment and NEP, they also point to complexities that may confound our interpretation of these productivity measures.

1. Introduction

Forests play a critical role in the global carbon cycle. Although details of the carbon cycle have long interested ecosystem ecologists, this interest has recently grown to include a wide range of researchers, forest managers, and policy makers as the link between atmospheric carbon dioxide (CO₂) and climate change becomes increasingly clear. Further, any efforts aimed at managing forests to partially mitigate elevated atmospheric CO₂ require a thorough understanding of the forest carbon cycle. Particularly important in our understanding of the forest carbon cycle is the inherent year-to-year variability in carbon sequestration. At the level of forest stands, annual carbon sequestration

is inferred primarily from tree growth (i.e., carbon assimilated to woody tissue) or from eddy covariance (i.e., CO₂ exchange between forest canopies and the atmosphere) measurements.

Tree growth is regularly monitored for ecological studies using repeated diameter measurements of sample trees, from which net primary productivity can be inferred (Clark et al., 2001). Changes in tree biomass estimated from repeated measurements can be used to calculate the mass of carbon fixed into plant tissue. However, repeated tree measurements on an annual basis are time intensive, costly, and prone to measurement error. An alternative to repeated measurements in temperate and boreal systems is utilizing annual tree-ring records (derived from increment cores) to reconstruct previous tree diameters.

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Annual diameter growth can then be converted to tree biomass growth (and hence carbon gain) using published allometric equations. This method has the potential to track annual stand-level forest productivity back decades, and more importantly does not require repeated field inventories (Dye et al., 2016).

Stand-level forest productivity can also be estimated using the eddy covariance (flux) technique (Baldocchi et al., 1988). Flux towers reaching above tree canopies continuously measure net CO₂ exchange at the canopy-atmosphere interface, with a footprint (i.e., flux measurement zone) ranging from hundreds of meters to several kilometers (Baldocchi 2003). These exchanges provide robust datasets capable of inferring year-to-year variability in net ecosystem productivity (NEP). As these datasets become more temporally robust, they can be used to track whole-forest response to climate variability (Hollinger et al., 2004; Wharton and Falk 2016) and disturbance (Ueyama et al., 2011; Hicke et al., 2012), and to improve ecosystem carbon dynamics models (Richardson et al., 2010). However, establishing and maintaining eddy flux towers requires sizeable financial and logistical investments.

Tree biomass increment expressed at the stand-level can potentially serve as a proxy for NEP (measured from eddy covariance); however, the two measures differ in magnitude because they provide information on different components of the ecosystem. NEP captures the cumulative, total difference between all CO₂ sources and sinks within the entire system. While trees are the largest sink contributing to NEP in forested systems, they do not necessarily represent the annual variability in carbon exchange from other components (e.g., saplings, understorey vegetation) nor carbon lost from respiration. As a result, tree biomass increment represents a subset of the carbon sink registered by NEP.

Naturally, we are led to ask to what extent the two methods for assessing productivity – tree biomass from tree-ring methods and NEP from eddy flux measures – are linked on annual timescales. If they track each other reliably, then tree-ring records could be calibrated to provide inferences about NEP for sites without flux towers. Eddy flux coupled with tree growth has been used to validate photosynthesis and transpiration rates (Catovsky et al., 2002) and to evaluate forest productivity response to climate (Grant et al., 2009; Wharton and Falk 2016). However, previous attempts to link annual NEP with tree diameter growth (Rocha et al., 2006; Zweifel et al., 2010) and tree biomass increment (Babst et al., 2013; Delpierre et al., 2016) have produced inconsistent results. For example, Babst et al. (2013) demonstrate positive correlations between tree biomass increment and early season flux measurements (January–July), yet Delpierre et al. (2016) suggest the two metrics are uncorrelated on an annual basis. These studies have been limited in part because of relatively short eddy-flux time series.

Discrepancies between tree biomass increment and NEP measurements may be due to temporary non-structural carbohydrate storage (Gough et al., 2009; Babst et al., 2013; Delpierre et al., 2016). Plants accumulate non-structural carbohydrates (primarily sugars and starch) via photosynthesis that can be mobilized and used for later growth or other plant functions (Chapin et al., 1990). Non-structural carbohydrates are critical for dormant season respiration and maintenance, and unused carbohydrates will often contribute to early season structural growth in the following year (Keel et al., 2006; Eglin et al., 2010; Michelot et al., 2011). Non-structural carbohydrate stores can last for several years; in some species they can remain in stemwood for over a decade (Richardson et al., 2013). As a result of carbohydrate storage, multi-year metrics of tree biomass increment, when compared to single-year tree biomass increment, appear to be more strongly correlated with NEP measurements (Barford et al., 2001; Curtis et al., 2002; Gough et al., 2008).

Our specific objective here was to characterize the relationship between annual tree biomass increment (from tree ring series) and annual NEP (from eddy covariance measurements). We conducted this work at the Howland Research Forest, a mature, mixed-species, multi-aged coniferous forest located in central Maine, USA. Howland has one

of the longest available eddy flux time series in the USA, extending back to 1996. This long time series allowed us to not only characterize the relationship between the two methods, but also to isolate potential lag-periods of tree growth and evaluate carbon allocation strategies, improving our understanding of the forest carbon cycle. Our work builds upon previous work by Babst et al. (2013) by examining the relationship in a more complex system and over a longer time period. Our study provides a framework for tracking annual forest carbon sequestration using tree-ring methods that can be used in future studies.

2. Methods

2.1. Site description

This study was conducted in the Howland Research Forest in central Maine, USA, which is widely recognized for its long-term research in forest ecosystem science (see Rustad and Fernandez 1998; Hollinger et al., 1999; Davidson et al., 2002; Richardson et al., 2009). The site has the second longest running flux record in the US, extending back to 1996 (the longest belonging to Harvard Forest). The 20 years of data used here provide a time series long enough for robust analyses of relationships between NEP and tree biomass increment.

The Howland Forest supports a mature multi-aged forest dominated by red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*), consisting of approximately 90% conifer, and 10% deciduous tree species (Table 1). Soils are spodosols, formed in well- to poorly-drained glacial till with very little elevational change. The climate is damp and cool, with average annual temperatures of 6.2 °C and a mean annual precipitation of 1148 mm (Daly et al., 2008). The site has evidence of previous logging (evenly distributed, well-decayed cut stumps) but has been unmanaged for roughly a century. Compared to other stands of the region, Howland Forest is diverse in both tree size and age distribution. The site supports several remnant trees in excess of 200 years old, along with many standing dead trees, and pit-and-mound topography.

A 3-ha permanent plot (150 × 200 m) whose center lies 240 m north of the main tower, was established in 1989 by the Laboratory for Terrestrial Physics at NASA's Goddard Space Flight Center for remote sensing and ecosystem dynamics research (see Weishampel et al., 1994; Ranson et al., 2001; Sun et al., 2011). At that time, all living and dead plot trees ≥ 3.0 cm diameter at breast height (DBH, 1.37 m) were mapped and measured (diameter and total height), recording ca. 7800 stems. Each tree was uniquely tagged for later re-measurement. This plot is subsequently referred to as the NASA plot. The tree species composition of the NASA plot – based on relative densities and relative basal areas (Table 1) – is nearly identical to that of the 46 continuous

Table 1

Forest descriptors by tree species in the Howland Forest NASA plot (2015 inventory). Species ranked by decreasing relative density based on trees ≥ 10 cm. (DBH = diameter at breast height; density refers to the number of trees per unit area.).

Species	Relative density	Relative basal area	DBH (cm)		
			Mean	Std. dev.	Max.
Red spruce (<i>Picea rubens</i>)	0.447	0.413	20.1	7.1	45.2
Eastern hemlock (<i>Tsuga canadensis</i>)	0.278	0.276	20.5	8.1	50.1
N. white-cedar (<i>Thuja occidentalis</i>)	0.108	0.086	18.8	6.4	40.9
Red maple (<i>Acer rubrum</i>)	0.090	0.069	18.2	6.7	41.3
White pine (<i>Pinus strobus</i>)	0.049	0.140	33.3	17.2	68.5
Balsam fir (<i>Abies balsamea</i>)	0.021	0.006	11.7	1.5	16.9
Yellow birch (<i>Betula alleghaniensis</i>)	0.004	0.007	25.8	12.5	56.3
Paper birch (<i>Betula papyrifera</i>)	0.003	0.003	19.0	7.5	31.5

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