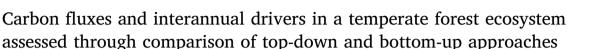
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ABSTRACT

Despite decades of research, gaining a comprehensive understanding of carbon (C) cycling in forests remains a considerable challenge. Uncertainties stem from persistent methodological limitations and the difficulty of resolving top-down estimates of ecosystem C exchange with bottom-up measurements of individual pools and fluxes. To address this, we derived estimates and associated uncertainties of ecosystem C fluxes for a 100–125 year old mixed temperate forest stand at the Bartlett Experimental Forest, New Hampshire, USA, using three different approaches: (1) tower-based eddy covariance, (2) a biometric approach involving C flux measurements of individual ecosystem subcomponents, and (3) an inventory approach involving changes in major C stocks over time. Our analysis made use of 13 years of data, collected over the period from 2004 to 2016.

Estimates of mean annual net ecosystem production (NEP) ranged from 120 to 133 g C m^{-2} , demonstrating strong agreement among methods and suggesting that this aging forest acts as a moderate C sink. The use of multiple approaches to measure C fluxes and their uncertainties helped place constraints on difficult-to-measure processes such as aboveground contributions to ecosystem respiration and belowground allocation to mycorrhizal fungal biomass (which was estimated at 20% of net primary production).

Analysis of interannual variability in C fluxes revealed a decoupling between annual wood growth and either current year or lagged NEP or GPP, suggesting that source limitation (C supply) is likely not controlling rates of wood production, at least on an interannual scale. Results also demonstrated a strong association between the maximum rate of C uptake during the growing season (Amax) and the length of the vernal window, defined as the period of time between soil thaw and the onset of photosynthesis. This suggests an important, but poorly understood, influence of winter and spring climate on mid-summer canopy physiology. Efforts to resolve the mechanisms responsible should be prioritized in light of ongoing and predicted changes in climate for the northeastern U.S. region, particularly during the winter and winter-spring transition period.

1. Introduction

Forests represent the dominant land cover type in the northeastern United States (Foster and Aber, 2004) and are widely regarded as carbon sinks given their state of recovery from widespread agriculture in the 19th century (Caspersen et al., 2000; Goodale et al., 2002). However, the ability of these aging secondary forests to continue to act as net carbon sinks as they transition to late-successional stands is unclear. Although a commonly accepted view is that old-growth forests are carbon neutral (Odum, 1969), more recent reviews indicate that late successional forests can often act as net carbon sinks (Luyssaert et al., 2008). Additional data on the net carbon flux of eastern North American forests should improve our understanding of the ability of these forests to continue to act as net carbon sinks.

Approaches to estimating net C exchange in forests include eddy covariance flux towers, biometric estimates of growth and respiration, and changes in important C stocks over time. Each of these has inherent strengths and limitations. Eddy flux towers provide direct measurements of net CO_2 exchange at high temporal resolution, but can suffer from unquantified advective losses (e.g. Aubinet et al., 2012; Novick

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et al., 2014; van Gorsel et al., 2009; Vickers et al., 2012), data gaps during calm periods, and non-CO₂ C fluxes. Eddy flux measurements also lack information on how C is allocated to various ecosystem components (e.g. foliage, wood, fine roots, mycorrhizal fungi), that possess a range of functions and C residence times and that are required to more fully test ecosystem models.

Biometric approaches that quantify the difference between net primary production (NPP) and heterotrophic respiration (R_h), can provide independent estimates of net ecosystem C exchange and can shed light on how C is allocated among various pools. However, this requires estimates of difficult-to-measure fluxes (e.g. belowground biomass production), which can introduce substantial uncertainties (Clark et al., 2001)

Estimating net C exchange from changes in major C stocks offer yet another approach, the benefits of which include its straightforward nature and lack of reliance on difficult-to-measure fluxes. However, belowground C pools are large and notoriously variable, making change detection extremely difficult (Vadeboncoeur et al., 2012). And, on its own, this method doesn't offer insight into mechanisms or subcomponent C fluxes. Consistency between top-down and bottom-up C quantification approaches can greatly enhance confidence in estimates of an ecosystem's C balance. Taken together, data from multiple approaches can also provide estimates on a full suite of ecosystem C fluxes to which ecosystem models can be more thoroughly compared.

Here we used multiple methodological approaches to compile a comprehensive carbon budget for an aging (100–125 year old) mixed temperate forest in New England (Bartlett Experimental Forest, NH). This included a comparison of net and gross ecosystem C fluxes using 3 complementary approaches (eddy covariance, biometric estimates of NPP and R_h, and a modified C inventory approach) for 13 years (2004–2016) of data. We included estimates of uncertainty for all three approaches, and highlight how the comparison of several independent methodological approaches provided more confidence in estimates of difficult-to-measure respiratory and belowground fluxes. Finally, drivers of interannual variations of C fluxes were evaluated by comparing net ecosystem production (NEP), gross primary production (GPP), ecosystem respiration (Re), and wood growth to an array of climatic, phenological, and biological variables.

2. Methods

2.1. Site description

Bartlett Experimental Forest (BEF) (44°06'N, 71°3'W) is located within the White Mountain National Forest in north-central New Hampshire, USA (Fig. 1). The climate is humid continental with cool

summers (mean July temperature, 19 °C) and cold winters (mean January temperature, -9 °C). Mean annual temperature is 6 °C and mean annual precipitation is 1270 mm (for additional site information, see http://www.fs.fed.us/ne/durham/4155/bartlett.htm). The forest within the eddy covariance tower footprint was cutover circa 1900 and some areas were damaged by the 1938 hurricane. In the past decade there has also been small-scale forest management just outside the tower footprint, but mean stand age is roughly 100-125 years. Average canopy height is approximately 20-22 m within the tower footprint and is composed of a diverse assemblage of species including Acer rubrum (29%), Fagus grandifolia (25%), Tsuga canadensis (14%), Betula alleghaniensis (9%), Betula papyrifera (6%), Fraxinus americana (5%), Acer saccharum (5%), and Populus grandidentata (4%), with minor amounts of other coniferous species. Soils are generally acidic Spodosols and Inceptisols derived from granitic till, and poor in both Ca and P (Vadeboncoeur et al., 2014). Foliar N and ecosystem N cycling rates are both low relative to other mixed hardwood sites in the region (Ollinger et al., 2002).

In 2003, BEF was adopted as a NASA North American Carbon Program (NACP) Tier-2 field research and validation site. During this time a 26.5 m tower was installed in a low-elevation (290 m) mixed hardwood stand for the purpose of making eddy covariance measurements of the forest-atmosphere exchange of carbon dioxide, water, and sensible heat. Continuous flux and meteorological measurements began in January 2004 and are ongoing (data are available online from AmeriFlux, http://www.public.ornl.gov/ameriflux/). In 2004, 12 FIAstyle plots (Hollinger, 2008) were established across a 1 km by 1 km area centered on the flux tower for the purpose of making complimentary biometric measurements of carbon pools and fluxes. BEF is also a NEON relocatable site (construction began in the summer of 2013) and the new flux tower is located within 100 m of the existing flux tower.

2.2. Eddy covariance estimates of C flux and uncertainty

The eddy covariance system provides direct measurements of the net ecosystem exchange rate of CO_2 between the forest canopy and the atmosphere (NEE). Eddy covariance estimates of NEE, after accounting for a change in sign, are equivalent to net ecosystem production (NEP_{EC}) assuming that sources and sinks of inorganic C are negligible (Chapin et al., 2006).

Forest-atmosphere CO_2 flux (NEE) was measured at a height of 25 m with an eddy covariance system consisting of a model SAT-211/3 K 3- axis sonic anemometer (Applied Technologies, Longmont, Colo.) and ducted to a model LI-6262 CO_2/H_2O infrared gas analyzer (Li-Cor, Lincoln, Neb.), through 2500 cm of 0.476 cm ID polyethylene tubing at

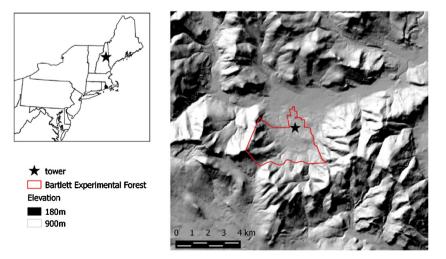


Fig. 1. A) Location of Bartlett Experimental Forest (BEF); B) Representation of topography surrounding BEF.

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