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# **Carbon fluxes and interannual drivers in a temperate forest ecosystem assessed through comparison of top-down and bottom-up approaches**

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# 1 **Abstract**

2 Despite decades of research, gaining a comprehensive understanding of carbon (C)  
3 cycling in forests remains a considerable challenge. Uncertainties stem from persistent  
4 methodological limitations and the difficulty of resolving top-down estimates of  
5 ecosystem C exchange with bottom-up measurements of individual pools and fluxes. To  
6 address this, we derived estimates and associated uncertainties of ecosystem C fluxes for  
7 a 100-125 year old mixed temperate forest stand at the Bartlett Experimental Forest, New  
8 Hampshire, USA, using three different approaches: (1) tower-based eddy covariance, (2)  
9 a biometric approach involving C flux measurements of individual ecosystem  
10 subcomponents, and (3) an inventory approach involving changes in major C stocks over  
11 time. Our analysis made use of 13 years of data, collected over the period from 2004 to  
12 2016.

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

19         Analysis of interannual variability in C fluxes revealed a decoupling between  
20 annual wood growth and either current year or lagged NEP or GPP, suggesting that  
21 source limitation (C supply) is likely not controlling rates of wood production, at least on  
22 an interannual scale. Results also demonstrated a strong association between the  
23 maximum rate of C uptake during the growing season (A<sub>max</sub>) and the length of the

24 vernal window, defined as the period of time between soil thaw and the onset of  
25 photosynthesis. This suggests an important, but poorly understood, influence of winter  
26 and spring climate on mid-summer canopy physiology. Efforts to resolve the  
27 mechanisms responsible should be prioritized in light of ongoing and predicted changes  
28 in climate for the northeastern U.S. region, particularly during the winter and winter-  
29 spring transition period.

30

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## 32 **1. Introduction**

33 Forests represent the dominant land cover type in the northeastern United States (Foster  
34 and Aber. 2004) and are widely regarded as carbon sinks given their state of recovery  
35 from widespread agriculture in the 19<sup>th</sup> century (Caspersen et al., 2000; Goodale et al.,  
36 2002). However, the ability of these aging secondary forests to continue to act as net  
37 carbon sinks as they transition to late-successional stands is unclear. Although a  
38 commonly accepted view is that old-growth forests are carbon neutral (Odum, 1969),  
39 more recent reviews indicate that late successional forests can often act as net carbon  
40 sinks (Luyssaert et al., 2008). Additional data on the net carbon flux of eastern North  
41 American forests should improve our understanding of the ability of these forests to  
42 continue to act as net carbon sinks.

43       Approaches to estimating net C exchange in forests include eddy covariance flux  
44 towers, biometric estimates of growth and respiration, and changes in important C stocks  
45 over time. Each of these has inherent strengths and limitations. Eddy flux towers  
46 provide direct measurements of net CO<sub>2</sub> exchange at high temporal resolution, but can  
47 suffer from unquantified advective losses (e.g. Aubinet et al., 2012; Novick et al., 2014;  
48 van Gorsel et al., 2009; Vickers et al., 2012), data gaps during calm periods, and non-CO<sub>2</sub>  
49 C fluxes. Eddy flux measurements also lack information on how C is allocated to various  
50 ecosystem components (e.g. foliage, wood, fine roots, mycorrhizal fungi), that possess a  
51 range of functions and C residence times and that are required to more fully test  
52 ecosystem models.

53       Biometric approaches that quantify the difference between net primary production  
54 (NPP) and heterotrophic respiration ( $R_h$ ), can provide independent estimates of net

55 ecosystem C exchange and can shed light on how C is allocated among various pools.  
56 However, this requires estimates of difficult-to-measure fluxes (e.g. belowground  
57 biomass production), which can introduce substantial uncertainties (Clark et al., 2001)

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

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

## 78 **2. Methods**

### 79 **2.1. Site description**

80 Bartlett Experimental Forest (BEF) (44°06'N, 71°3'W) is located within the White  
81 Mountain National Forest in north-central New Hampshire, USA (Figure 1). The climate  
82 is humid continental with cool summers (mean July temperature, 19°C) and cold winters  
83 (mean January temperature, -9°C). Mean annual temperature is 6°C and mean annual  
84 precipitation is 1270 mm (for additional site information, see  
85 <http://www.fs.fed.us/ne/durham/4155/bartlett.htm>). The forest within the eddy  
86 covariance tower footprint was cutover circa 1900 and some areas were damaged by the  
87 1938 hurricane. In the past decade there has also been small-scale forest management  
88 just outside the tower footprint, but mean stand age is roughly 100-125 years. Average  
89 canopy height is approximately 20–22 m within the tower footprint and is composed of a  
90 diverse assemblage of species including *Acer rubrum* (29%), *Fagus grandifolia* (25%),  
91 *Tsuga canadensis* (14%), *Betula alleghaniensis* (9%), *Betula papyrifera* (6%), *Fraxinus*  
92 *americana* (5%), *Acer saccharum* (5%), and *Populus grandidentata* (4%), with minor  
93 amounts of other coniferous species. Soils are generally acidic Spodosols and Inceptisols  
94 derived from granitic till, and poor in both Ca and P (Vadeboncoeur et al., 2014). Foliar  
95 N and ecosystem N cycling rates are both low relative to other mixed hardwood sites in  
96 the region (Ollinger et al., 2002).

97 In 2003, BEF was adopted as a NASA North American Carbon Program (NACP)  
98 Tier-2 field research and validation site. During this time a 26.5 m tower was installed in  
99 a low-elevation (290 m) mixed hardwood stand for the purpose of making eddy



100 covariance measurements of the forest–atmosphere exchange of carbon dioxide, water,  
101 and sensible heat. Continuous flux and meteorological measurements began in January,  
102 2004 and are ongoing (data are available online from AmeriFlux,  
103 <http://www.public.ornl.gov/ameriflux/>). In 2004, 12 FIA-style plots (Hollinger, 2008)  
104 were established across a 1 km by 1 km area centered on the flux tower for the purpose of  
105 making complimentary biometric measurements of carbon pools and fluxes. BEF is also  
106 a NEON relocatable site (construction began in the summer of 2013) and the new flux  
107 tower is located within 100 meters of the existing flux tower.

## 108 **2.2. Eddy covariance estimates of C flux and uncertainty**

109 The eddy covariance system provides direct measurements of the net ecosystem  
110 exchange rate of CO<sub>2</sub> between the forest canopy and the atmosphere (NEE). Eddy  
111 covariance estimates of NEE, after accounting for a change in sign, are equivalent to net  
112 ecosystem production (NEP<sub>EC</sub>) assuming that sources and sinks of inorganic C are  
113 negligible (Chapin III et al., 2006).

114 Forest–atmosphere CO<sub>2</sub> flux (NEE) was measured at a height of 25 m with an  
115 eddy covariance system consisting of a model SAT-211/3K 3- axis sonic anemometer  
116 (Applied Technologies, Longmont, Colo.) and ducted to a model LI-6262 CO<sub>2</sub>/H<sub>2</sub>O  
117 infrared gas analyzer (Li-Cor, Lincoln, Neb.), through 2500 cm of 0.476 cm ID  
118 polyethylene tubing at 75 cc s<sup>-1</sup> with data recorded at 5 Hz and fluxes (covariances)  
119 calculated every 30 minutes. In 2014 the LI-6262 was replaced with a model LI-7200  
120 analyzer. Average (30 minute) meteorological variables (e.g. air and soil temperatures,  
121 incoming solar radiation, etc.) measured at the tower were recorded concurrently. The  
122 instrument configuration, calibration protocol, QA/QC, and data processing procedures

123 were identical to those used at the Howland AmeriFlux site in central Maine, USA, and  
124 have been documented in detail elsewhere (Hollinger et al., 2004). Site visits by the  
125 AmeriFlux Tech Team took place in the summers 2006 and 2016, to confirm overall  
126 quality of the flux and meteorological measurements.

127 Half-hourly NEE data were filtered to remove time periods with low atmospheric  
128 turbulence where advective losses were likely significant similar to Barr et al. (2013).  
129 Following this approach a median  $u^*$  threshold of  $0.50 \pm 0.10$  was detected and used  
130 across all seasons and years. Gaps in NEE were filled using the (Barr et al., 2004)  
131 Fluxnet-Canada method (FCM) with slight modifications, including: mild exclusion of  
132 NEE outliers; use of a weighted mean of soil and air temperature as the independent  
133 variable for estimating  $R_e$ ; and delineation of nighttime periods from global shortwave  
134 radiation of less than  $5 \text{ W m}^2$ . Random uncertainties in NEE were estimated following  
135 (Richardson and Hollinger, 2007). NEE was partitioned into gross primary production  
136 ( $GPP_{EC}$ ) and total ecosystem respiration ( $R_{eEC}$ ) using the FCM method. Further details  
137 of the gap-filling and partitioning methods used are presented in Barr et al. (2013).

### 138 **2.3. Biometric estimates of carbon fluxes with uncertainty**

139 In addition to eddy covariance, we used measurements of individual ecosystem  
140 components to make biometric estimates of gross and net carbon fluxes. For biometric  
141 estimates of NEP, ( $NEP_B$ ), we subtracted heterotrophic respiration ( $R_h$ ), including  
142 respiration from dead woody biomass ( $R_{DW}$ ), and the heterotrophic portion of soil  
143 respiration ( $R_{SH}$ ), from total net primary production (NPP), including NPP from foliage,  
144 aboveground woody tissues, understory production, fine and coarse roots, and  
145 mycorrhizae (Table 1). We also calculated biometric estimates of gross primary

146 production ( $GPP_B$ ) and ecosystem respiration ( $Re_B$ ).  $GPP_B$  was calculated by summing  
147 all sources of NPP, with all sources of autotrophic respiration, including autotrophic  
148 respiration from foliage, aboveground wood, and the autotrophic portion of soil  
149 respiration (Table 1). Biometric estimates of  $Re_B$  were calculated by summing all  
150 sources of heterotrophic and autotrophic respiration including total soil respiration,  
151 respiration from coarse woody debris and standing dead wood, as well as from foliar and  
152 woody tissues.

### 153 **2.3.1. Aboveground production**

154 Beginning in 2004 estimates of aboveground carbon pools and fluxes were made on 12  
155 plots within a 1 km by 1 km area centered on the flux tower with a similar layout, but  
156 larger size, to that described in Hollinger (2008). Each of the 12 plots contains four 10 m  
157 radius subplots for a total of 48 subplots within the 1 km<sup>2</sup> footprint of the flux tower.  
158 Each subplot contains 3 soil respiration collars, 2 litterfall traps, and 1 branchfall  
159 collection tarp, resulting in 154 soil respiration collars, 96 litterfall traps, and 48  
160 branchfall collection tarps within the 1 km<sup>2</sup> footprint around the flux tower. We followed  
161 established methods for estimating woody biomass and production (Clark et al., 2001;  
162 Curtis, 2008), litterfall and branchfall (Bernier et al., 2008), and biomass of coarse woody  
163 debris (Valentine et al., 2008).

164 In each of the 48 subplots within the 1 km<sup>2</sup> footprint of the flux tower the  
165 location, diameter at breast height (dbh), and species of all trees greater than 12.7 cm  
166 were recorded annually from 2004-2016. For small trees (2.54 to 12.7 cm dbh), all trees  
167 were measured within a 2 m radius microplot within each subplot, with microplot center  
168 4 meters (at an azimuth of 90°) from subplot center. Dbh measurements on all trees were

169 made each year after leaf fall in late October/early November by the same three person  
170 team using paint markings to improve the consistency of repeat measurements.

171 To calculate the NPP of live woody tissues (both large and small trees), estimates  
172 of live woody biomass of the previous year were subtracted from current year estimates,  
173 while holding the dbh of any trees that died throughout the study period constant at the  
174 last live measurement as recommended in Clark et al. (2001). Above and belowground  
175 woody NPP and associated uncertainty were then calculated using a Monte Carlo  
176 simulation approach similar to that described by Yanai et al. (2010). This approach  
177 estimates the statistical distribution of the output of a calculation through multiple  
178 iterations in which the input data are chosen randomly based on their underlying  
179 distributions. Specifically for each iteration the measured diameter of each tree was  
180 allowed to vary randomly with a normal distribution using standard deviation (s.d.) of 0.1  
181 cm. The percent carbon (%C) of woody material was varied randomly for both  
182 hardwood species (mean of 48% and s.d. of 1%) and for coniferous species (mean of  
183 50% and s.d. of 1%). Because many allometric equations lack estimates of error, we  
184 simulated uncertainty due to allometric modeling by randomly selecting between 3  
185 different sets of allometric models. Two local species specific allometric models  
186 (Whittaker et al., 1974; Young et al., 1980), and one set of generalized (taxonomically  
187 grouped) allometric models (Chojnacky et al., 2014) were chosen randomly for each  
188 iteration. For each iteration, %C and choice of allometric model were held constant for  
189 all years. The mean and 95% confidence interval of 1000 iterations were used to derive  
190 NPP (difference between current and previous year woody biomass), and associated  
191 uncertainty measurements for each subplot for each year. Uncertainties from the Monte

192 Carlo simulations were propagated with spatial (plot to plot) and temporal variability  
193 using classical error propagation techniques (see Section 2.6.).

194 Annual branchfall collections were used to calculate a mean estimate of the  
195 contribution of branchfall to woody carbon flux, while annual foliar and fruit/flower  
196 collections were used to calculate a mean estimate of carbon flux to foliar/fruit/flower  
197 production. Branchfall (<5 cm diameter) was collected once per year in October, using  
198 one 3.34 m<sup>2</sup> branchfall tarp on each subplot for a total of 48 branchfall tarps. Annual  
199 foliar and fruit/flower production were estimated by collection of aboveground litterfall  
200 using 2 litterfall traps (0.24 m<sup>2</sup>) randomly placed in each subplot. Litter was collected 2-  
201 5 times each fall and once the following spring. To convert branchfall and litterfall into  
202 C fluxes, annual biomass collections were multiplied by the mean %C (49%).  
203 Uncertainty due to %C, spatial variability, and temporal variability were summed using  
204 standard error propagation techniques (using a 2% standard error for %C) and reported as  
205 95% confidence intervals.

206 The contribution of understory production to total NPP was estimated using  
207 allometric models and annual seedling surveys on 2 meter diameter microplots in each of  
208 the 48 subplots, following methods described in (Chojnacky and Milton, 2008).  
209 Uncertainty due to spatial and temporal variation as well as uncertainties in %C were  
210 propagated using standard techniques.

### 211 **2.3.2. Belowground production**

212 Production of fine roots (<2 mm diameter) was estimated using ingrowth cores. Within  
213 the tower footprint, 90 individual year-long (late October 2013 – late October 2014) cores  
214 were installed to 30 cm depth. Total root mass per area found in the ingrowth cores was

215 assumed to represent annual fine root production. Estimates were not corrected for the  
216 tendency of cores to overestimate root biomass or to account for root growth below 30  
217 cm depth. Omitting these two biases likely has a small effect on estimates of root  
218 production; Park et al. (2007) found that in stands at Bartlett Experimental Forest cores  
219 tended to overestimate by 27% (compared to soil pits) while sampling to only 30 cm led  
220 to a 28% underestimate of root biomass. Uncertainty due to spatial variation and %C  
221 ( $49\% \pm 2\%$ ), were propagated using standard error propagation techniques.

222 Estimates of ectomycorrhizal (ECM) fungal production were made using a stable  
223 isotope approach described in (Hobbie and Hobbie, 2008; Ouimette et al., 2013). Briefly,  
224 ECM fungi discriminate against  $^{15}\text{N}$  during the creation of nitrogen (N) transfer  
225 compounds for plant hosts. The fraction of nitrogen transferred to ECM hosts (Tr) can be  
226 calculated (eq. 1), using the fractionation factor during mycorrhizal transfer of N ( $\Delta f$ ),  
227 and the  $^{15}\text{N}:^{14}\text{N}$  ratios (expressed as  $\delta^{15}\text{N}$ ) in plant ( $\delta^{15}\text{N}_{\text{Plant}}$ ) and soil available N  
228 ( $\delta^{15}\text{N}_{\text{Avail}}$ ).

229

$$230 \quad \text{Tr} = 1 + (\delta^{15}\text{N}_{\text{Plant}} - \delta^{15}\text{N}_{\text{Avail}})/\Delta f \quad (1)$$

231

232 The amount of C allocated to ECM fungal biomass can then be calculated  
233 stoichiometrically (eq. 2) using the fraction of N transferred to plant host (Tr), plant host  
234 N demand, and the C:N ratio of fungi as:

235

$$236 \quad \text{NPP}_{\text{fungi}} = (1/\text{Tr} - 1) \times \text{N}_{\text{demand}} \times \text{C}/\text{N}_{\text{fungi}} \times f_{\text{ECM}} \quad (2)$$

237

238 where  $N_{\text{demand}}$  is annual plant N demand,  $C/N_{\text{fungi}}$  is the C/N ratio of ECM fungi, and  $f_{\text{ECM}}$   
239 is the biomass fraction of ECM trees within the stand. Here we used the  $\delta^{15}\text{N}$  of co-  
240 located (by depth) root and soil samples to calculate  $\text{Tr}$ , net annual changes in foliar,  
241 wood, and fine root N stocks to calculate plant N demand.

242 As an alternative approach to assess our estimates of mycorrhizal production we  
243 compared biometric estimates of NEP to estimates of NEP from eddy covariance and C  
244 inventory approaches. Specifically, production of mycorrhizal fungi was initially  
245 included as a component of  $\text{NEP}_B$  ( $\text{NEP}_B$  was calculated as total NPP minus the  
246 heterotrophic portion of ecosystem respiration – Table 1). We additionally calculated  
247  $\text{NEP}_B$  omitting our measured mycorrhizal fungal C flux. To do this we ran Monte Carlo  
248 simulations (10,000 iterations) to calculate  $\text{NEP}_B$ , allowing estimates of each component  
249 of NPP and  $R_h$  to vary with their measured/estimated distributions (similar to Yanai et  
250 al., 2010). Estimates of  $\text{NEP}_B$  that both included and omitted our estimate of mycorrhizal  
251 NPP were compared to NEP estimates from eddy covariance and C inventory  
252 approaches.

253 Additionally, we estimated total belowground carbon allocation (TBCA) using the  
254 mass balance approach described in Raich and Nadelhoffer (1989) and Davidson et al.  
255 (2002). Specifically, TBCA was estimated as the difference between total soil respiration  
256 and fine litterfall. This approach assumes that changes in the stocks of soil organic  
257 matter, roots, and litter are in near steady state or small relative to soil respiration and  
258 litterfall.

### 259 **2.3.3. Soil respiration**

260 Soil respiration was measured using infra-red gas analyzers (IRGA) in conjunction with  
261 both static chambers and autochambers. The static chambers consisted of a 10 inch PVC  
262 collar permanently inserted ~5 cm into the soil. Three collars per subplot (144 chambers  
263 across the 1 km<sup>2</sup> tower footprint) were measured roughly every 3 weeks during the snow-  
264 free portion of each year using a LICOR 820 CO<sub>2</sub> gas analyzer during 2004-2007 (>3400  
265 measurements). Simultaneous soil moisture and temperature measurements were made at  
266 5 cm soil depth. Chamber volumes were measured every year but were approximately  
267 5.5 liters. After scrubbing the chamber to ~30 ppm below ambient CO<sub>2</sub> concentrations,  
268 concentrations were measured every 2 seconds over a 60 second period. The flux was  
269 calculated as follows: flux (umoles CO<sub>2</sub> m<sup>-2</sup> sec<sup>-1</sup>) = PV/RTA \* (dxCO<sub>2</sub>/dt), where P is  
270 chamber pressure in bar, V is chamber volume in m<sup>3</sup>, T is chamber air temperature in  
271 Kelvin, A is chamber area in m<sup>2</sup>, R is the ideal gas law constant or 0.0000834472 m<sup>3</sup>·bar  
272 K<sup>-1</sup>·mole<sup>-1</sup>, and (dxCO<sub>2</sub>/dt) is the rate of change of the mole fraction CO<sub>2</sub> concentration in  
273 the chamber (umoles sec<sup>-1</sup>).

274 During 2007-2008 five autochambers were operated on a single plot continuously  
275 during the snow-free periods of the year (>5600 measurements) following methods  
276 described in (Phillips et al., 2010).

277 To derive annual soil CO<sub>2</sub> flux estimates for both static and autochambers,  
278 measured CO<sub>2</sub> flux rates from the chambers were fit using a Gauss-Newton optimization  
279 method in JMP 13.0 statistical software (SAS 2016), to a suite of respiration models  
280 (Richardson et al., 2006) including Q<sub>10</sub> temperature, temperature and time varying Q<sub>10</sub>,  
281 soil water content modulated Q<sub>10</sub>, Arrhenius, and logistic response functions. For most  
282 models, fit parameters did not vary significantly between years for either static or



283 autochambers (results not shown), thus measurements from all years were pooled to  
284 derive modeled parameters for each chamber type.

285 Model best fits (using data from 2004-2008) were applied to continuous (every 30  
286 min) temperature and moisture measurements made at the base of the eddy covariance  
287 flux tower (5 cm depth) to estimate annual soil CO<sub>2</sub> flux rates for each chamber type  
288 during all years (2004-2016). Lower and upper 95% confidence intervals were estimated  
289 for each model and chamber type. Since annual CO<sub>2</sub> flux rates and model goodness of fit  
290 varied minimally among model types, results from a logistic fit are reported to minimize  
291 gap-filling artifacts between chamber-based soil respiration and eddy covariance tower-  
292 based ecosystem respiration estimates (also modeled logistically).

293 Soil CO<sub>2</sub> flux during winter months was estimated using the logistic fit (above),  
294 derived from measurements during the snow-free season. Because winter respiration  
295 fluxes can be similar in magnitude to NEP, a more direct estimate of wintertime  
296 respiration was also made during the winter of 2011-2012 using the soda lime technique  
297 described in Grogan (1998) and Keith and Wong (2006). Briefly, roughly 800 g of oven-  
298 dried, soda lime were left from November 17, 2011 to March 21, 2012 (125 days), in an  
299 enclosed chamber (surface area = 0.06783 m<sup>2</sup>). All post-collection soda lime weights  
300 were blank-corrected using the mean of 6 field blanks prior to flux calculation. Because  
301 estimates of winter respiration using the soda lime technique (data not shown) were  
302 similar to those estimated using a logistic fit from chamber measurements, soil CO<sub>2</sub> flux  
303 during winter months was estimated using the logistic temperature response model  
304 described above.

305 To scale up to the forest stand, chamber-based soil CO<sub>2</sub> flux measurements were  
306 corrected for the area occupied by rocks and tree root crowns (roughly 13%) similar to  
307 Bae et al. (2015). Uncertainty was estimated by propagating uncertainty due to soil  
308 rockiness, model fit, as well as spatial and temporal variability.

#### 309 **2.3.4. Partitioning R<sub>s</sub> into autotrophic and heterotrophic components**

310 No attempt was made to directly measure the contribution of autotrophic (R<sub>SA</sub>) or  
311 heterotrophic (R<sub>SH</sub>) respiration to total soil respiration (R<sub>S</sub>). Instead we used several  
312 different approaches to partition R<sub>S</sub>. First, the Global Database of Soil Respiration  
313 Version 3 (Bond-Lamberty and Thomson, 2014) was used to derive a relationship  
314 between R<sub>SH</sub> and R<sub>S</sub>. We used data from non-experimentally manipulated, temperate,  
315 deciduous, forest ecosystems with quality check flags of Q0, Q01, Q02, and Q03 (n =  
316 114) to derive the following relationship between annual R<sub>SH</sub> and R<sub>S</sub>:  $R_{SH} = 1.925$   
317  $(\pm 34.392) + R_S * 0.534 (\pm 0.045)$ . This relationship was used with measured estimates of  
318 mean annual R<sub>S</sub> to derive annual estimates of R<sub>SH</sub> (and R<sub>SA</sub> by difference). Monte Carlo  
319 simulations using the uncertainty in annual R<sub>S</sub> and in the relationship between R<sub>S</sub> and R<sub>SH</sub>  
320 were used to estimate uncertainty in R<sub>SH</sub> and R<sub>A</sub> and reported as 95% confidence  
321 intervals as described above. As an additional approach to help assess the uncertainty in  
322 estimates of R<sub>SH</sub>, we estimated R<sub>SH</sub> independently by summing all detritus inputs  
323 (branchfall, foliar litterfall and root and mycorrhizal production) following (Bond-  
324 Lamberty et al., 2004). This independent approach was compared to estimates of R<sub>SH</sub>  
325 using the partitioning method described above.

326 **2.3.5. Respiration from woody biomass**

327 To estimate annual respiratory losses from dead woody material, estimates of dead  
328 woody C stocks were multiplied by the mean decay rate for hardwood species from  
329 Russell et al. (2014) (hardwood species comprised 97% of the standing dead woody  
330 biomass pool). Dead woody biomass was assumed to have 49% C (Thomas and Martin,  
331 2012) with a standard error of 2%. Uncertainty due to initial estimates of dead woody  
332 biomass, %C, and decay rates from Russell et al. (2014) were propagated using standard  
333 error propagation techniques and reported as 95% confidence intervals.

334 No direct measurements of respiration from live woody biomass were made.  
335 Instead, we used two approaches to estimate losses of CO<sub>2</sub> from live woody biomass.  
336 First, to derive a “biometric” estimate that was independent of eddy covariance  
337 measurements, live woody respiration was assumed to be equal to 0.118 of biometric  
338 GPP, the median ratio of woody respiration to GPP of mature and old growth forests (>  
339 50 years old; n = 16) reported in the database of (Litton et al., 2007). Uncertainty was  
340 reported as 0.75 of the mean annual flux.

341 Additionally, we derived estimates of aboveground respiration (including foliage  
342 and live and dead woody biomass) as the annual difference between eddy covariance  
343 estimates of ecosystem respiration and soil respiration from chamber measurements.

344 **2.3.6. Foliar respiration**

345 Dark respiration for live foliage was estimated using species-specific leaf-level  
346 measurements of dark respiration and scaled to the stand and annual scales using  
347 estimates of stand leaf area index (LAI) and a temperature sensitive Q<sub>10</sub> response  
348 function. Specifically, gas exchange measurements of dark respiration were conducted

349 during August of 2014 and July/August of 2016 on cloud-free days between 1000 - 1500  
350 EST using a portable gas exchange system (LICOR-6400xt, LICOR, Lincoln, NE, USA),  
351 equipped with a standard 2 × 3 cm leaf cuvette and a LICOR-6400-02B LED light  
352 source. During measurements [CO<sub>2</sub>] was maintained at a value of 400 ppm, relative  
353 humidity at 50%, and temperature held constant at a temperature of 24.5°C (reference  
354 temperature). Species-specific estimates of foliar dark respiration (n=75 across all  
355 species) were then weighted by the fractional contribution of each species to stand LAI to  
356 derive a stand-level dark respiration rate at the reference temperature (Rd<sub>ref</sub>).

357 A Q10 response function (eq. 3) was used to estimate dark respiration rates at  
358 temperatures other than the reference temperature using Rd<sub>ref</sub> and half hourly  
359 measurements of air temperature (periods when PAR < 5 umoles m<sup>-2</sup> sec<sup>-1</sup>), where for eq.  
360 3, T<sub>air</sub> and T<sub>ref</sub>, were the measured air temperature and reference air temperature  
361 (24.5°C), respectively.

362

$$363 \text{ Foliar dark respiration rate} = \text{Rd}_{\text{ref}} \times \text{Q}_{10}^{(\text{T}_{\text{air}} - \text{T}_{\text{ref}})} \quad (3)$$

364

365 Because the Q10 temperature response function of foliar dark respiration is known to  
366 vary over short timescales with changes in ambient temperature, Q10 was allowed to vary  
367 with ambient temperature following (Tjoelker et al., 2001;  $\text{Q}_{10} = 3.22 - 0.046 * \text{air}$   
368 temperature). Annual stand-level foliar dark respiration rates were then made by  
369 multiplying temperature adjusted dark respiration rates by estimates of stand LAI  
370 summing half hourly estimates.

371           Uncertainty due to variation in leaf-level dark respiration rates, as well as  
372 uncertainty in estimates LAI and the temperature response function reported in (Tjoelker  
373 et al., 2001) were quantified using Monte Carlo simulations as described above where  
374 estimates of each parameter were allow vary with their measured distributions.

375

## 376 **2.4. Changes in carbon stocks ( $\Delta C$ )**

377 To complement eddy covariance and biometric estimates of NEP, we estimated the mean  
378 annual change in total ecosystem carbon stocks ( $\Delta C$ ) using a modified carbon inventory  
379 approach. Inventory approaches rely on knowing the carbon stock of various ecosystem  
380 pools at two points in time. In closed-canopy forest stands, the pools of primary  
381 importance are live and dead woody biomass, as well as soil carbon. Here we focus on  
382 changes in woody carbon stocks and assume that changes in soil carbon stocks were  
383 minimal as was found from measurements at mature stands in nearby Hubbard Brook  
384 Experimental Forest (Yanai et al., 2013). Changes in soil carbon stocks would be very  
385 difficult to detect over a 13 year study period (Vadeboncoeur et al., 2012). Instead, in  
386 these mature (100-125 year old) stands we assumed that there was little to no net change  
387 in annual soil C stocks; however, we included an uncertainty of  $\pm 40 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Post  
388 and Kwon, 2000).

389           To estimate changes in woody carbon stocks, we used a modified inventory  
390 approach. First, in 2004, we made initial measurements of standing live and dead woody  
391 biomass using the allometric approach described above (Section 2.3.1), except that  
392 standing dead woody biomass was adjusted using species- and decay-class specific  
393 density reduction factors from Harmon et al. (2011), and structural loss adjustment

394 factors from Domke et al. (2011). In 2004 we also made estimates of dead woody  
395 biomass in coarse woody debris (CWD) using field surveys. For all downed woody  
396 material > 7.6 cm, estimates of CWD decay class and volume were estimated using 3  
397 methods: line intersect sampling (LIS), modified transect relascope sampling (MTRS),  
398 and fixed plot sampling, see Pesonen et al. (2009) and Valentine et al. (2008) for details  
399 of each method type. For the present study, two 100 meter transects (LIS), one 1 meter  
400 transect (MTRS), or four 1 m<sup>2</sup> subplots per each of the 12 FIA style plots were sampled.  
401 CWD volume was then multiplied by species- and decay class- specific density values  
402 from Harmon et al. (2008) to estimate CWD biomass. Total dead woody biomass in  
403 2004 was estimated as the sum of CWD and standing dead pools.

404         Because we had only a single measurement of standing dead biomass and CWD  
405 in 2004, we estimated changes in dead woody biomass using annual inputs to the dead  
406 woody pool (from known live tree death and measured branchfall), while accounting for  
407 loss of carbon through decay from standing and downed dead wood using a decay rate of  
408 0.0467 (the weighted average of the rates reported in Russell et al. (2014) for hardwoods  
409 and conifers based on the proportion of standing dead wood in our plots). To derive the  
410 mean annual change in total ecosystem carbon stocks ( $\Delta C$ ) we assumed the  
411 predominantly angiosperm woody biomass was comprised of 49% C with a standard  
412 error of 2% (Thomas and Martin, 2012). Uncertainty due to initial estimates of dead  
413 woody biomass, %C, and decay rates from Russell et al. (2014), and the assumption of no  
414 changes in soil C stocks were propagated using standard error propagation techniques and  
415 reported as 95% confidence intervals.

## 416 **2.5. Potential drivers of interannual variability**

417 To investigate the potential drivers of interannual variation in woody NPP, NEE, GPP,  
418 and Re, we used a suite of meteorological and phenological parameters measured at the  
419 flux tower including incoming total, direct, and diffuse photosynthetically active  
420 radiation (PAR), air and soil temperature, soil thaw day, precipitation, relative humidity,  
421 vapor pressure deficit, soil moisture content, the length, start and end dates of periods of  
422 gross and net carbon uptake, as well as the length of the vernal window - defined here as  
423 the number of days between soil thaw and the onset of gross carbon uptake (where mean  
424 daily  $GPP_{EC}$  averaged over a 7 day period, exceeded  $4 \text{ umoles CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$ ). We also  
425 calculated a drought index by counting the number of growing season days where the  
426 volumetric water content (VWC) was less than 17.5%; a value that represented 50% of  
427 the growing season mean during 2004-2016. In addition to these meteorological and  
428 phenological parameters we collected data on biochemical and biological parameters  
429 including annual concentrations of foliar nitrogen (estimated following Smith et al.  
430 (2008)) and masting years from Potter et al. (2015). Annual estimates of growing season  
431 canopy level  $A_{max}$  and dark respiration ( $R_d$ ) from the eddy flux data were estimated  
432 using a light response curve (eq. 4). For this analysis, all high-quality (ustar-filtered,  
433 non-gapfilled) measurements of half hourly NEP during June-August were used with  
434 measured PAR to estimate model parameters (e.g.  $A_{max}$ ,  $R_d$ ).

$$435 \quad NEP = \frac{a * PAR}{\left( \left( 1 - \frac{PAR}{2000} \right) + \frac{a * PAR}{A_{max}} \right)} - R_d \quad (4)$$

436 where PAR was the measured incoming photosynthetically active radiation and  $a$  was the  
437 quantum yield.

438 Both current year and 1 year lagged annual and seasonal data from these metrics  
439 were compared to measured C fluxes using stepwise linear multiple regression analysis  
440 with AIC (Akaike information criterion) to identify significant relationships.

## 441 **2.6. Statistical Methods and Uncertainty Propagation**

442 To combine estimates of uncertainty from various sources (e.g. temporal, spatial,  
443 analytical, etc.) standard uncertainty propagation techniques were used. Specifically, to  
444 add sources of uncertainty the following approach was taken:

$$445 \quad SE_{(x+y)} = \sqrt{(SE_x)^2 + (SE_y)^2} \quad (5)$$

446 Where SE is standard error of component x, y, or (x + y). 95% confidence intervals were  
447 then estimated as 1.96 \* SE.

## 448 **3. Results**

### 449 **3.1. Estimated carbon fluxes using multiple approaches**

#### 450 **3.1.1. Multiyear mean fluxes**

451 Estimates and associated uncertainties of mean ecosystem C fluxes during 2004-2016 are  
452 shown in Table 1 and include components of NPP, respiratory fluxes, and estimates of  
453 NEP, GPP, and Re. Mean (2004-2016) estimates of  $NEP_{EC}$ ,  $NEP_B$ , and  $\Delta C$  ranged from  
454 120-133 g C m<sup>-2</sup> yr<sup>-1</sup>, indicating surprising consistency in multiyear mean estimates of  
455 ecosystem net carbon flux across top-down and bottom-up approaches. All three  
456 approaches indicate that this aging 100-125 year old stand is a moderate carbon sink.  
457 Eddy covariance and biometric estimates of mean (2004-2016) GPP and Re also differed



458 by less than 5% and were statistically indistinguishable. Total belowground carbon  
459 allocation (calculated as soil respiration minus fine litterfall) was estimated at  $656 \pm 54$  g  
460  $\text{C m}^{-2} \text{ yr}^{-1}$ , within the range reported for stands of similar age within BEF (620-681 g C  
461  $\text{m}^{-2} \text{ yr}^{-1}$ ) (Bae et al., 2015).

462 The magnitude of uncertainty in NEP, GPP, and Re differed across approaches.  
463 For estimates of NEP, eddy covariance ( $132 \pm 49$  g C  $\text{m}^{-2} \text{ yr}^{-1}$ ) and inventory ( $133 \pm 34$  g  
464  $\text{C m}^{-2} \text{ yr}^{-1}$ ) approaches had much lower uncertainty than biometric estimates of NEP ( $120$   
465  $\pm 156$  g C  $\text{m}^{-2} \text{ yr}^{-1}$ ). Uncertainty in eddy covariance estimates originate both from the  
466 measurements themselves as well as filtering and gapfilling procedures. Estimates of the  
467 uncertainty due to potential biases in the selection of a ustar filter were not included and  
468 would increase the reported uncertainty (Figure 2). Uncertainty in biometric estimates of  
469 NEP are largely driven by uncertainties in fine root and mycorrhizal NPP as well as the  
470 heterotrophic portion of soil respiration (17%, 36%, and 42% of total error respectively).

471 Because estimates of the production of mycorrhizal fungi are lacking from many  
472 forest C budget efforts, we also used Monte Carlo simulations to calculate  $\text{NEP}_B$   
473 excluding our mycorrhizal C flux estimates, using only mean fluxes and uncertainty from  
474 the other components of  $\text{NEP}_B$ . Excluding our estimates of mycorrhizal production  
475 resulted in  $\text{NEP}_B$  near zero ( $-3 \pm 123$  g C  $\text{m}^{-2} \text{ yr}^{-1}$ ), and an inconsistency between  $\text{NEP}_B$   
476 and both  $\text{NEP}_{EC}$  and  $\Delta C$ .

### 477 **3.1.2 Components of NPP**

478 Mean annual NPP was estimated at  $615 \pm 118$  g C  $\text{m}^{-2} \text{ yr}^{-1}$ . Growth of woody biomass  
479 including aboveground components of large and small trees, and replacement of

480 branchfall comprised approximately 33% of total NPP ( $238 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). Annual  
481 production of foliage, fruits, flowers, and seedlings was estimated at  $143 \pm 15 \text{ g C m}^{-2} \text{ yr}^{-1}$   
482 or 23% of total NPP. This value may be an underestimate due to removal of seeds from  
483 litter baskets by small mammals. Estimates of fine root production and production of  
484 mycorrhizae were  $110 \pm 64$  and  $124 \pm 93 \text{ g C m}^{-2} \text{ yr}^{-1}$ , respectively, and, along with  
485 coarse woody roots, resulted in a belowground production estimate that was 44% of total  
486 NPP. Uncertainties in estimated belowground C fluxes to mycorrhizae are unknown, but  
487 are likely to be large. If we set this value at 75% of our measured estimate, then  
488 uncertainties in belowground fluxes (including fine root production) accounted for 94%  
489 of the uncertainty in total NPP.

### 490 **3.1.3. Respiratory Fluxes**

491 Estimates of autotrophic and heterotrophic components of soil  $\text{CO}_2$  flux, as well as  
492 respiration from woody biomass and foliage are shown in Table 1. Soil respiration  
493 represented the largest component of ecosystem respiration at  $810 \pm 48 \text{ g C m}^{-2} \text{ yr}^{-1}$ .  
494 Estimates of soil respiration from manual chambers and autochambers were within 5% of  
495 one another and annual estimates were relatively insensitive to the type of model used to  
496 scale instantaneous measurements to annual fluxes (data not shown). Modelled winter  
497 fluxes from manual and autochambers were similar to estimates over the same time  
498 period using a soda lime technique (data not shown). Annual soil respiration estimates  
499 are also within the range estimated at similar stands elsewhere within the Bartlett  
500 Experimental Forest ( $790\text{-}864 \text{ g C m}^{-2} \text{ yr}^{-1}$ ; Bae et al., 2015).

501 The heterotrophic portion of soil respiration (using the partitioning approach  
502 described above) was estimated at  $434 \pm 101 \text{ g C m}^{-2} \text{ yr}^{-1}$ , and was the largest

503 heterotrophic component of ecosystem respiration. In comparison, independent estimates  
504 of  $R_{SH}$  from summing inputs of detritus were  $388 \text{ g C m}^{-2} \text{ yr}^{-1}$ . This value is within the  
505 uncertainty but lower than our estimates of  $R_{SH}$  using the partitioning approach. In the  
506 ecosystem is roughly in steady state with regards to soil inputs and outputs, then  
507 estimates of  $R_{SH}$  made by summing detrital inputs are likely underestimates because they  
508 exclude inputs from incorporation of CWD and root exudates. Heterotrophic respiration  
509 from aboveground dead woody biomass was estimated at  $61 \pm 12 \text{ g C m}^{-2} \text{ yr}^{-1}$ .

510         The autotrophic portion of soil respiration was the largest component of  
511 autotrophic ecosystem respiration (55%) at  $376 \pm 101 \text{ g C m}^{-2} \text{ yr}^{-1}$ . Autotrophic  
512 respiration from foliage and live woody material together make up 45% of total  
513 autotrophic respiration, estimated at  $149 \pm 20$  and  $153 \pm 114 \text{ g C m}^{-2} \text{ yr}^{-1}$ , respectively.

514         Measurements of the components of ecosystem respiration include soil respiration  
515 as well as aboveground foliar and woody respiration. We had measurements for total soil  
516 respiration and foliar respiration but lacked direct measurements of respiration from  
517 aboveground woody material. To assess the consistency of our estimates of aboveground  
518 woody respiration with estimates of other measured carbon fluxes in this system, we  
519 compared mean daily estimates of  $R_{eEC}$  to soil respiration ( $R_s$ ), to estimate respiration  
520 from aboveground components  $R_{abv}$ . The difference between mean annual  $R_{eEC}$  and  $R_s$   
521 was  $343 \text{ g C m}^{-2} \text{ yr}^{-1}$ , or ~30% of  $R_{eEC}$  (Figure 3a). In comparison, the sum of our  
522 estimates of aboveground live foliar and woody autotrophic, as well as dead woody  
523 heterotrophic respiration from biometric estimates totaled  $363 \text{ g C m}^{-2} \text{ yr}^{-1}$ , roughly 31%  
524 of  $R_{eEC}$ .

### 525 **3.2. Interannual variation and climate drivers**

526 Considerable interannual variation in several meteorological and phenological variables  
527 occurred over the 13 year period (2004-2016) used to calculate mean C fluxes. For  
528 example, mean annual air temperature varied by nearly 2°C, mean spring (Julian days 76-  
529 135) and early summer (Julian days 136-215) air temperatures by more than 3°C, and  
530 mean winter air temperature by more than 6°C. Variables related to the start of the  
531 growing season also differed significantly over the 13 year period with variations in soil  
532 thaw day of more than a month, the onset of gross carbon uptake by more than 2 weeks,  
533 and the length of the vernal window by more than 5 weeks. In addition, growing season  
534 precipitation ranged from 279 to 680 mm, while the number of growing season days with  
535 a mean volumetric water content (VWC) less than 17.5% ranged from 0 to 42 days per  
536 year.

537         Interannual variation in eddy covariance estimates of GPP, Re, and NEP during  
538 this 13-year period varied by  $\pm 9\%$ ,  $\pm 12\%$ , and  $\pm 80\%$  around their means, respectively.  
539 We used stepwise multiple regression and model averaging to identify the phenological  
540 and meteorological parameters that were most strongly related to interannual variation in  
541 C fluxes (e.g. Hui et al., 2003). Using simple regression approaches, a majority of the  
542 interannual variation in  $GPP_{EC}$  were captured using a two-parameter model ( $r^2 = .83$   $p <$   
543  $0.0001$ ) that included growing season soil temperature (negative correlation) and total  
544 incoming PAR during the growing season (positive correlation) - the two parameters that  
545 were used to parameterize the gap filling models employed for  $Re_{EC}$  and  $GPP_{EC}$ ,  
546 respectively. Similarly, interannual variation in  $Re_{EC}$  was most strongly related to  
547 fluctuations in mean annual soil temperature (positive correlation).

548           Because of the predominance of gap-filled estimates in computing annual sums,  
549 we took a second approach to assess potential controls on interannual C flux variability  
550 using only high quality, half-hourly NEE data to parameterize a simple Michaelis-Menten  
551 light-response model. Interannual variation in modelled parameter estimates of canopy  
552 level maximum gross carbon uptake ( $A_{max}$ ) and dark respiration ( $R_d$ ) were regressed  
553 against meteorological and phenological variables.

554           The strongest correlation with growing season (June-August)  $A_{max}$ , was the  
555 length of the vernal window, defined here as the number of days between soil thaw and  
556 the start of the C uptake period ( $r^2 = 0.74$ ,  $p < 0.00031$ ; Figure 4b). Taken separately, soil  
557 thaw day was also significantly, positively correlated with  $A_{max}$  ( $r^2 = 0.44$ ,  $p = 0.019$ ;  
558 Figure 4a), while the start of C uptake was not ( $p = 0.12$ ). A longer vernal window (and  
559 an earlier soil thaw day) was correlated with a lower canopy  $A_{max}$ . Adding additional  
560 parameters did not result in an improved model and we did not detect a correlation  
561 between  $A_{max}$  and previous year net or gross C uptake at annual or seasonal time scales.  
562 Interannual variation in estimates of canopy-level dark respiration from the light-response  
563 model was positively correlated to  $A_{max}$  ( $r^2 = 0.69$ ,  $p = 0.0009$ ), and, showed a similar  
564 negative correlation with the length of the vernal window ( $r^2 = 0.47$   $p = 0.0014$

565           Annual wood growth (Figure 5a) was compared to both current-year and previous  
566 year meteorological and phenological variables as well as  $GPP_{EC}$  and  $NEP_{EC}$ , across a  
567 range of time periods (seasons). No significant relationship was detected between annual  
568 wood production and variations in gross or net carbon uptake from any time period  
569 (current-year or lagged). Instead wood growth was best predicted with a two parameter  
570 model that included early summer air temperature and the number of growing season

571 days with soil volumetric water content less than 17.5% ( $r^2 = 0.75$ ,  $p < 0.002$ , RMSE =  
572  $16.9 \text{ g C m}^{-2} \text{ yr}^{-1}$ ; Figure 5b), with higher wood growth rates occurring in warmer and  
573 wetter years.

## 574 **4. Discussion**

### 575 **4.1. Comparison of top-down and bottom-up approaches and** 576 **uncertainty using mean C fluxes**

577 Any technique for quantifying ecosystem-scale carbon dynamics has both strengths and  
578 limitations. Comparing top-down eddy covariance estimates of C exchange and bottom-  
579 up biometric estimates of C fluxes can serve as a valuable cross-validation tool, and can  
580 improve estimates of both an ecosystem's carbon balance as well as its components. At  
581 BEF, differences in 13 year mean (2004-2016) estimates of NEP, GPP, and Re between  
582 eddy covariance and biometric approaches were all within 10% of one another, indicating  
583 surprising consistency between methods despite large difference in their underlying  
584 sources of error. Consistency between eddy covariance and biometric approaches is  
585 often seen when comparing multiyear mean estimates. For example, at a secondary  
586 successional mixed northern hardwood forest in Michigan, the difference between NEP  
587 from eddy covariance and biometric approaches varied by up to 148% for individual  
588 years, but converged to within 1% of one another using 5 year mean estimates (Gough et  
589 al., 2008).

590 The agreement in eddy covariance and biometric C flux estimates at BEF  
591 provided confidence in estimates of difficult-to-measure C fluxes, and highlighted the  
592 advantage of complementary methodological approaches. For example, the flux tower at

593 BEF is situated within a valley at 250 m above sea level, and on all sides the surrounding  
594 land rises to >750 meters above sea level within 3 km of the flux tower (Figure 1). This  
595 topographic relief increases the potential for advective transport of CO<sub>2</sub>, which could lead  
596 to underestimates of C exchange measured at the top of the eddy covariance flux tower.  
597 Advective losses are a well-known challenge when using the eddy covariance technique  
598 and have been dealt with in several ways; the most common being the application of a  
599 *ustar* (friction velocity) threshold filter to exclude data when atmospheric turbulence is  
600 not developed enough to minimize horizontal advective transport (Aubinet, 2008; Aubinet  
601 et al., 2012). Following the *ustar* filter threshold selection approach of Barr et al. (2013),  
602 the high *ustar* threshold determined at BEF (0.5 m s<sup>-1</sup>), in addition to other data gaps  
603 resulted in exclusion of >90% of available nighttime data (Figure 2). Despite this  
604 tradeoff in data quantity, using only high quality, *ustar* filtered data, resulted in good  
605 agreement with biometric approaches.

606         The use of biometric data to estimate NEP, GPP, and Re requires estimates of C  
607 flux to several ecosystem pools that are extremely difficult to measure. At BEF  
608 aboveground fluxes of net primary production are relatively well-constrained, while  
609 belowground C fluxes to fine roots and especially mycorrhizal fungi have higher  
610 uncertainty. However, not including estimates of these difficult-to-measure fluxes  
611 resulted in an inconsistency between biometric and eddy covariance estimates of gross  
612 and net C fluxes. In lieu of making individual estimates of fine root and mycorrhizal  
613 production, a mass balance approach to estimate total belowground carbon allocation  
614 (TBCA) described in (Davidson et al., 2002), can be used, although it does not  
615 distinguish between fine root and mycorrhizal fungi production. This approach assumes

616 that soil carbon stocks are at or near steady state and requires only estimates of soil  
617 respiration and aboveground fine litterfall. At BEF, TBCA was estimated at  $656 \pm 54$  g C  
618  $\text{m}^{-2} \text{yr}^{-1}$ , similar to estimates of the sum of coarse and fine root production, mycorrhizal  
619 production, and soil autotrophic respiration,  $644$  g C  $\text{m}^{-2} \text{yr}^{-1}$ .

620 Estimates of aboveground foliar and woody respiration are also difficult to  
621 constrain given their biological control and temporal heterogeneity. The difference  
622 between estimates of ecosystem respiration and soil respiration is a mass balance  
623 approach that can estimate respiration of aboveground ecosystem components (Giasson et  
624 al., 2013). At BEF, this approach yielded similar results ( $343$  g C  $\text{m}^{-2} \text{yr}^{-1}$ ) to our initial  
625 estimates of aboveground respiration ( $363 \pm 117$  g C  $\text{m}^{-2} \text{yr}^{-1}$ ). This mass balance  
626 approach also yields estimates at a fine temporal resolution and may capture important  
627 phenological events (Davidson et al., 2006). At BEF estimates of  $R_{\text{abv}}$  using this mass  
628 balance approach highlight the phenological influence on aboveground respiration, with  
629  $R_{\text{abv}}$  contributing a relatively large proportion of  $R_{\text{e}}$  during spring leaf out (and the onset  
630 of wood growth) and during autumn leaf senescence (Figure 3b).

631 The consistency of our initial C flux estimates with mass balance approaches that  
632 used soil respiration, aboveground litterfall, and  $R_{\text{EC}}$  to calculate TBCA and  $R_{\text{abv}}$ ,  
633 demonstrate the benefit of including these as routine data streams at eddy covariance  
634 network sites. Including soil respiration and litterfall measurements at flux sites provides  
635 valuable information on both above and belowground ecosystem C fluxes allowing for  
636 not only cross validation of ecosystem C fluxes but the ability to more rigorously test  
637 ecosystem models (McFarlane et al., 2014; Phillips et al., 2017).



## 638 **4.2. Interannual variation**

### 639 **4.2.1 GPP, Re, Amax**

640 Interannual variations in GPP, Re, NEP, and parameters describing light response  
641 functions are determined by both direct and indirect drivers, and have the potential to  
642 provide insight into how ecosystems might respond under future climate. A complication  
643 in understanding the drivers of interannual C variation from eddy covariance is the  
644 abundance of gap-filled data. At BEF, on average, 90-95% of nighttime and nearly 50%  
645 of daytime fluxes during the growing season were gap-filled. It is thus not surprising that  
646 interannual variation in gap-filled  $GPP_{EC}$  and  $Re_{EC}$  were strongly related to temperature  
647 and incoming PAR, the two variables used to parameterize the gap-filling models.

648         Although short term (hours to days) changes in temperature and PAR are  
649 frequently correlated to short term variations in C fluxes (and hence why they are used in  
650 gap-filling models), they may not be directly related to interannual variation in C fluxes.  
651 Several studies have shown the importance of variation in the biotic response to abiotic  
652 drivers, especially for regulating interannual carbon flux variation (Richardson et al.,  
653 2007). Data from BEF support a similar conclusion. For example, using only high-  
654 quality, raw (not gap-filled) data, the strong relationship between growing season canopy  
655  $A_{max}$  (and  $R_d$ ) and the length of the vernal window suggests that indirect mechanisms  
656 (biotic responses) are important in regulating canopy C exchange.

657         Mechanisms through which the length of the vernal window can influence canopy  
658 photosynthesis are not well understood. In the northeastern US, a longer vernal window  
659 has been correlated to winters with a reduced snowpack (Contosta et al., 2016). Other  
660 studies have repeatedly linked reduced snowpack to an increase in soil freeze-thaw events

661 and increases in the loss of nutrients through both dissolved and gaseous pathways  
662 (Matzner and Borken, 2008; Song et al., 2017). For example, at the Hubbard Brook  
663 Experimental Forest (40 km west of BEF), both experimental (Campbell et al., 2014;  
664 Fitzhugh et al., 2001) and observational studies across a climate gradient (Durán et al.,  
665 2016) have shown increased losses of nitrogen and decreased N availability following  
666 winters with reduced snowpack. Whether decreases in soil nutrient availability prior to  
667 leaf out results in decreased foliar biomass, lower canopy nitrogen content, or reduced  
668 photosynthetic capacity is still unknown. However, leaf area index (LAI) is often limited  
669 by soil nutrients and water (Cowling and Field, 2003), and numerous studies have shown  
670 significant increases in foliar biomass and LAI following fertilization, e.g. Gower et al.  
671 (1992).

672 In addition to reductions in nutrient availability, earlier snowmelt has been shown  
673 to intensify forest hydrological cycles and increase springtime runoff (Creed et al., 2015).  
674 Late growing season water stress related to earlier snowmelt has also been suggested as  
675 the driver of decreases in peak growing season productivity in boreal forests (Buermann  
676 et al., 2013) and temperate forests of the western US (Hu et al., 2010). At BEF the length  
677 of the vernal window is negatively correlated to soil moisture during the month prior to  
678 leaf out ( $r^2 = 0.40$ ,  $p = 0.027$ ) but not to soil moisture during the late growing season ( $r^2 =$   
679  $0.17$ ,  $p = 0.16$ ). Although mechanisms relating growing season  $A_{max}$  to the length of the  
680 vernal window are not fully known, data from BEF suggest that winter and spring  
681 conditions can exert a strong influence over ecosystem C dynamics during the growing  
682 season.

683 A few studies in temperate forests have found lagged effects on C fluxes (e.g.  
684 Howland Experimental Forest, Maine; (Richardson et al., 2013)). At BEF we did not  
685 detect a correlation between prior year meteorological conditions or C uptake, with  
686 current year C fluxes. In other work at BEF, Carbone et al., (2013) found that in stem  
687 wood of *Acer rubrum* trees, the nonstructural carbohydrate pool included both fast  
688 (younger) and slow (older) cycling subpools that could support growth and respiration of  
689 woody tissues. The lack of a correlation we see between wood growth and prior year  
690 climate and C fluxes may in part be the result of the growth habit of foliage of tree  
691 species at BEF. At BEF foliage and new shoots of the majority of the dominant species  
692 within the flux tower footprint have an indeterminate growth habit, meaning that during  
693 and after spring leaf expansion from the winter bud, the shoot apex remains active and  
694 continues to initiate additional leaves and shoot internodes if conditions are favorable. Of  
695 the dominant species only American beech and sugar maple tend to have determinate  
696 type foliar and shoot growth, where the number of leaf buds (number of leaves) is  
697 determined at the end of the preceding growing season. Many ecosystem models allocate  
698 C to foliar growth based more on a determinant type growth.

#### 699 **4.2.2. Wood growth**

700 Despite the importance of wood growth for a variety of ecosystem services, we still do  
701 not fully understand the mechanisms controlling variability in wood growth and how they  
702 may respond under future climate scenarios. Evidence from broad-scale analyses suggest  
703 a tradeoff between C allocation to wood versus fine roots, reflecting a tradeoff between  
704 acquiring growth limiting nutrients and/or water and competition for space in the sunlit

705 canopy (Dybzinski et al., 2011; Litton et al., 2007). Whether this tradeoff at ecosystem  
706 scales occurs interannually within an ecosystem is unknown.

707         Alternatively, wood growth is often viewed as “source” (C supply) versus “sink”  
708 (C demand) limited (Körner, 2015). At broad spatial scales wood growth generally  
709 correlates to GPP (Litton et al., 2007). This is why wood growth in many terrestrial  
710 ecosystem models is primarily source-driven, where wood production is linked to the  
711 amount of gross photosynthesis. However, recent work has downplayed the importance  
712 of C source in controlling wood growth and has emphasized the importance of  
713 climatically sink-driven metabolic and phenological processes (Delpierre et al., 2016,  
714 2015; Guillemot et al., 2015; Körner, 2003). These studies indicate an earlier onset of  
715 xylogenesis, faster rates of cell division, and faster rates of cell division under warmer,  
716 wetter conditions.

717         Our inability to detect a correlation between wood growth and either GPP or NEP  
718 at BEF suggests that interannual variations in wood growth are likely not directly “source  
719 driven.” Instead, wood growth is more strongly related to early growing season air  
720 temperature and growing season soil water stress. At BEF, wood growth was higher  
721 during years with warmer air temperatures during the early growing season and in years  
722 with ample growing season soil moisture, consistent with metabolic/phenologically  
723 “sink” driven mechanisms. Further, at BEF Carbone et al. (2013) showed the importance  
724 of stored C to the growth and metabolism of woody biomass, indicating that C allocated  
725 towards wood growth relies on both recent photosynthate as well as internal reserve C  
726 pools derived from both older and recent photosynthates. At broad-scales allocation to  
727 wood growth is likely controlled by C source (GPP) as well as tradeoffs involved in

728 acquiring growth limiting nutrients, while metabolically driven mechanisms may be  
729 important in regulating interannual variability within a site.

## 730 **5. Conclusion**

731 Long-term datasets using multiple approaches to estimate ecosystem carbon fluxes can  
732 provide cross validation of difficult-to-measure fluxes as well as potential insight into  
733 mechanisms that may be regulating C fluxes. At BEF, top-down and bottom-up  
734 approaches to estimate gross and net C exchange agreed well at a multiyear scale and  
735 provided more confidence in several difficult-to-measure C fluxes such as aboveground  
736 components of ecosystem respiration and belowground allocation to mycorrhizal fungi.  
737 The results from BEF also suggest several potential relationships that may be important  
738 to understanding forest ecosystem C fluxes under future climate. These include potential  
739 indirect effects of winter and spring climate (vernal window) on growing season  
740 photosynthesis, as well as direct metabolic (sink-driven) mechanisms driven by growing  
741 season climate. Such mechanisms warrant future study to assess their importance and to  
742 allow for their potential inclusion in models aimed at predicting ecosystem C dynamics  
743 under future conditions.

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- 758 Aubinet, M., 2008. Eddy Covariance Co2 Flux Measurements in Nocturnal Conditions:  
759 An Analysis of the Problem. *Ecol. Appl.* 18, 1368–1378.  
760 <https://doi.org/10.1890/06-1336.1>
- 761 Aubinet, M., Feigenwinter, C., Heinesch, B., Laffineur, Q., Papale, D., Reichstein, M.,  
762 Rinne, J., Gorsel, E.V., 2012. Nighttime Flux Correction, in: Aubinet, M., Vesala,  
763 T., Papale, D. (Eds.), *Eddy Covariance*, Springer Atmospheric Sciences. Springer  
764 Netherlands, pp. 133–157. [https://doi.org/10.1007/978-94-007-2351-1\\_5](https://doi.org/10.1007/978-94-007-2351-1_5)
- 765 Bae, K., Fahey, T.J., Yanai, R.D., Fisk, M., 2015. Soil Nitrogen Availability Affects  
766 Belowground Carbon Allocation and Soil Respiration in Northern Hardwood  
767 Forests of New Hampshire. *Ecosystems* 1–13. [https://doi.org/10.1007/s10021-](https://doi.org/10.1007/s10021-015-9892-7)  
768 [015-9892-7](https://doi.org/10.1007/s10021-015-9892-7)
- 769 Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., Nesic, Z., 2004. Inter-  
770 annual variability in the leaf area index of a boreal aspen-hazelnut forest in  
771 relation to net ecosystem production. *Agric. For. Meteorol.* 126, 237–255.  
772 <https://doi.org/10.1016/j.agrformet.2004.06.011>
- 773 Barr, A.G., Richardson, A.D., Hollinger, D.Y., Papale, D., Arain, M.A., Black, T.A.,  
774 Bohrer, G., Dragoni, D., Fischer, M.L., Gu, L., Law, B.E., Margolis, H.A.,  
775 McCaughey, J.H., Munger, J.W., Oechel, W., Schaeffer, K., 2013. Use of change-  
776 point detection for friction–velocity threshold evaluation in eddy-covariance  
777 studies. *Agric. For. Meteorol.* 171–172, 31–45.  
778 <https://doi.org/10.1016/j.agrformet.2012.11.023>
- 779 Bernier, P., Hanson, P.J., Curtis, P.S., 2008. Measuring Litterfall and Branchfall, in:  
780 Hoover, C.M. (Ed.), *Field Measurements for Forest Carbon Monitoring*. Springer  
781 Netherlands, pp. 91–101. [https://doi.org/10.1007/978-1-4020-8506-2\\_7](https://doi.org/10.1007/978-1-4020-8506-2_7)
- 782 Bond-Lamberty, B., Thomson, A., 2014. A global database of soil respiration data,  
783 Version 3.0. Data Set Available -Line [Httpdaacornl.gov](http://daacornl.gov) Oak Ridge Natl. Lab.  
784 Distrib. Act. Arch. Cent. Oak Ridge Tenn. USA  
785 [Httpdxdoiorg103334ORNLDAAC1235](http://dx.doi.org/10.3334/ORNLDAAC/1235).
- 786 Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. A global relationship between the  
787 heterotrophic and autotrophic components of soil respiration? *Glob. Change Biol.*  
788 10, 1756–1766. <https://doi.org/10.1111/j.1365-2486.2004.00816.x>
- 789 Buermann, W., Bikash, P.R., Jung, M., Burn, D.H., Reichstein, M., 2013. Earlier springs  
790 decrease peak summer productivity in North American boreal forests. *Environ.*  
791 *Res. Lett.* 8, 024027. <https://doi.org/10.1088/1748-9326/8/2/024027>
- 792 Campbell, J.L., Soggi, A.M., Templer, P.H., 2014. Increased nitrogen leaching following  
793 soil freezing is due to decreased root uptake in a northern hardwood forest. *Glob.*  
794 *Change Biol.* 20, 2663–2673. <https://doi.org/10.1111/gcb.12532>
- 795 Carbone, M.S., Czimczik, C.I., Keenan, T.F., Murakami, P.F., Pederson, N., Schaberg,  
796 P.G., Xu, X., Richardson, A.D., 2013. Age, allocation and availability of  
797 nonstructural carbon in mature red maple trees. *New Phytol.* 200, 1145–1155.  
798 <https://doi.org/10.1111/nph.12448>
- 799 Caspersen, J.P., Pacala, S.W., Jenkins, J.C., Hurtt, G.C., Moorcroft, P.R., Birdsey, R.A.,  
800 2000. Contributions of Land-Use History to Carbon Accumulation in U.S.  
801 Forests. *Science* 290, 1148–1151. <https://doi.org/10.1126/science.290.5494.1148>

802 Chapin III, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M.,  
803 Baldocchi, D.D., Clark, D.A., Harmon, M.E., Schimel, D.S., Valentini, R., Wirth,  
804 C., Aber, J.D., Cole, J.J., Goulden, M.L., Harden, J.W., Heimann, M., Howarth,  
805 R.W., Matson, P.A., McGuire, A.D., Melillo, J.M., Mooney, H.A., Neff, J.C.,  
806 Houghton, R.A., Pace, M.L., Ryan, M.G., Running, S.W., Sala, O.E., Schlesinger,  
807 W.H., Schulze, E.-D., 2006. Reconciling Carbon-cycle Concepts, Terminology,  
808 and Methods. *Ecosystems* 9, 1041–1050. [https://doi.org/10.1007/s10021-005-](https://doi.org/10.1007/s10021-005-0105-7)  
809 [0105-7](https://doi.org/10.1007/s10021-005-0105-7)

810 Chojnacky, D.C., Heath, L.S., Jenkins, J.C., 2014. Updated generalized biomass  
811 equations for North American tree species. *Forestry* 87, 129–151.  
812 <https://doi.org/10.1093/forestry/cpt053>

813 Chojnacky, D.C., Milton, M., 2008. Measuring Carbon in Shrubs, in: Hoover, C.M. (Ed.),  
814 Field Measurements for Forest Carbon Monitoring. Springer Netherlands, pp. 45–  
815 72. [https://doi.org/10.1007/978-1-4020-8506-2\\_5](https://doi.org/10.1007/978-1-4020-8506-2_5)

816 Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J.,  
817 2001. Measuring net primary production in forests: concepts and field methods.  
818 *Ecol. Appl.* 11, 356–370. [https://doi.org/10.1890/1051-](https://doi.org/10.1890/1051-0761(2001)011[0356:MNPPIF]2.0.CO;2)  
819 [0761\(2001\)011\[0356:MNPPIF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0356:MNPPIF]2.0.CO;2)

820 Contosta, A.R., Adolph, A., Burchsted, D., Burakowski, E., Green, M., Guerra, D.,  
821 Albert, M., Dibb, J., Martin, M., McDowell, W.H., Routhier, M., Wake, C.,  
822 Whitaker, R., Wollheim, W., 2016. A longer vernal window: the role of winter  
823 coldness and snowpack in driving spring transitions and lags. *Glob. Change Biol.*  
824 n/a-n/a. <https://doi.org/10.1111/gcb.13517>

825 Cowling, S.A., Field, C.B., 2003. Environmental control of leaf area production:  
826 Implications for vegetation and land-surface modeling. *Glob. Biogeochem.*  
827 *Cycles* 17, 1007. <https://doi.org/10.1029/2002GB001915>

828 Creed, I.F., Hwang, T., Lutz, B., Way, D., 2015. Climate warming causes intensification  
829 of the hydrological cycle, resulting in changes to the vernal and autumnal  
830 windows in a northern temperate forest. *Hydrol. Process.* 29, 3519–3534.  
831 <https://doi.org/10.1002/hyp.10450>

832 Curtis, P.S., 2008. Estimating Aboveground Carbon in Live and Standing Dead Trees, in:  
833 Hoover, C.M. (Ed.), Field Measurements for Forest Carbon Monitoring. Springer  
834 Netherlands, pp. 39–44. [https://doi.org/10.1007/978-1-4020-8506-2\\_4](https://doi.org/10.1007/978-1-4020-8506-2_4)

835 Davidson, E.A., Richardson, A.D., Savage, K.E., Hollinger, D.Y., 2006. A distinct  
836 seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a  
837 spruce-dominated forest. *Glob. Change Biol.* 12, 230–239.  
838 <https://doi.org/10.1111/j.1365-2486.2005.01062.x>

839 Davidson, E.A., Savage, K., Bolstad, P., Clark, D.A., Curtis, P.S., Ellsworth, D.S.,  
840 Hanson, P.J., Law, B.E., Luo, Y., Pregitzer, K.S., Randolph, J.C., Zak, D., 2002.  
841 Belowground carbon allocation in forests estimated from litterfall and IRGA-  
842 based soil respiration measurements. *Agric. For. Meteorol., FLUXNET 2000*  
843 *Synthesis* 113, 39–51. [https://doi.org/10.1016/S0168-1923\(02\)00101-6](https://doi.org/10.1016/S0168-1923(02)00101-6)

844 Delpierre, N., Berveiller, D., Granda, E., Dufrière, E., 2016. Wood phenology, not carbon  
845 input, controls the interannual variability of wood growth in a temperate oak  
846 forest. *New Phytol.* 210, 459–470. <https://doi.org/10.1111/nph.13771>



847 Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T., Rathgeber,  
848 C.B.K., 2015. Temperate and boreal forest tree phenology: from organ-scale  
849 processes to terrestrial ecosystem models. *Ann. For. Sci.* 73, 5–25.  
850 <https://doi.org/10.1007/s13595-015-0477-6>

851 Domke, G.M., Woodall, C.W., Smith, J.E., 2011. Accounting for density reduction and  
852 structural loss in standing dead trees: Implications for forest biomass and carbon  
853 stock estimates in the United States. *Carbon Balance Manag.* 6, 14.  
854 <https://doi.org/10.1186/1750-0680-6-14>

855 Durán, J., Morse, J.L., Groffman, P.M., Campbell, J.L., Christenson, L.M., Driscoll, C.T.,  
856 Fahey, T.J., Fisk, M.C., Likens, G.E., Melillo, J.M., Mitchell, M.J., Templer,  
857 P.H., Vadeboncoeur, M.A., 2016. Climate change decreases nitrogen pools and  
858 mineralization rates in northern hardwood forests. *Ecosphere* 7, n/a-n/a.  
859 <https://doi.org/10.1002/ecs2.1251>

860 Dybzinski, R., Farris, C., Wolf, A., Reich, P.B., Pacala, S.W., 2011. Evolutionarily  
861 Stable Strategy Carbon Allocation to Foliage, Wood, and Fine Roots in Trees  
862 Competing for Light and Nitrogen: An Analytically Tractable, Individual-Based  
863 Model and Quantitative Comparisons to Data. *Am. Nat.* 177, 153–166.  
864 <https://doi.org/10.1086/657992>

865 Fitzhugh, R.D., Driscoll, C.T., Groffman, P.M., Tierney, G.L., Fahey, T.J., Hardy, J.P.,  
866 2001. Effects of soil freezing disturbance on soil solution nitrogen, phosphorus,  
867 and carbon chemistry in a northern hardwood ecosystem. *Biogeochemistry* 56,  
868 215–238. <https://doi.org/10.1023/A:1013076609950>

869 Giasson, M.-A., Ellison, A.M., Bowden, R.D., Crill, P.M., Davidson, E.A., Drake, J.E.,  
870 Frey, S.D., Hadley, J.L., Lavine, M., Melillo, J.M., Munger, J.W., Nadelhoffer,  
871 K.J., Nicoll, L., Ollinger, S.V., Savage, K.E., Steudler, P.A., Tang, J., Varner,  
872 R.K., Wofsy, S.C., Foster, D.R., Finzi, A.C., 2013. Soil respiration in a  
873 northeastern US temperate forest: a 22-year synthesis. *Ecosphere* 4, 1–28.  
874 <https://doi.org/10.1890/ES13.00183.1>

875 Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A.,  
876 Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S., Nabuurs, G.-J., Nilsson, S.,  
877 Shvidenko, A.Z., 2002. Forest carbon sinks in the northern hemisphere. *Ecol.*  
878 *Appl.* 12, 891–899. [https://doi.org/10.1890/1051-0761\(2002\)012\[0891:FCSITN\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0891:FCSITN]2.0.CO;2)

880 Gough, C.M., Vogel, C.S., Schmid, H.P., Su, H.-B., Curtis, P.S., 2008. Multi-year  
881 convergence of biometric and meteorological estimates of forest carbon storage.  
882 *Agric. For. Meteorol., Chequamegon Ecosystem-Atmosphere Study Special*  
883 *Issue: Ecosystem-Atmosphere Carbon and Water Cycling in the Temperate*  
884 *Northern Forests of the Great Lakes Region* Great Lakes Region Special Issue  
885 148, 158–170. <https://doi.org/10.1016/j.agrformet.2007.08.004>

886 Gower, S.T., Vogt, K.A., Grier, C.C., 1992. Carbon Dynamics of Rocky Mountain  
887 Douglas-Fir: Influence of Water and Nutrient Availability. *Ecol. Monogr.* 62, 43–  
888 65. <https://doi.org/10.2307/2937170>

889 Grogan, P., 1998. CO<sub>2</sub> flux measurement using soda lime: correction for water formed  
890 during CO<sub>2</sub> adsorption. *Ecology* 79, 1467–1468. [https://doi.org/10.1890/0012-9658\(1998\)079\[1467:CFMUSL\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1467:CFMUSL]2.0.CO;2)

891

892 Guillemot, J., Martin-StPaul, N.K., Dufrêne, E., François, C., Soudani, K., Ourcival,  
893 J.M., Delpierre, N., 2015. The dynamic of the annual carbon allocation to wood in  
894 European tree species is consistent with a combined source–sink limitation of  
895 growth: implications for modelling. *Biogeosciences* 12, 2773–2790.

896 Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., 2008. Woody detritus density and  
897 density reduction factors for tree species in the United States: a synthesis.

898 Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., Yatkov, M., 2011. Differences  
899 between standing and downed dead tree wood density reduction factors: A  
900 comparison across decay classes and tree species.

901 Hobbie, E.A., Hobbie, J.E., 2008. Natural Abundance of <sup>15</sup>N in Nitrogen-Limited  
902 Forests and Tundra Can Estimate Nitrogen Cycling Through Mycorrhizal Fungi:  
903 A Review. *Ecosystems* 11, 815. <https://doi.org/10.1007/s10021-008-9159-7>

904 Hollinger, D.Y., 2008. Defining a Landscape-Scale Monitoring Tier for the North  
905 American Carbon Program, in: Hoover, C.M. (Ed.), *Field Measurements for  
906 Forest Carbon Monitoring*. Springer Netherlands, pp. 3–16.  
907 [https://doi.org/10.1007/978-1-4020-8506-2\\_1](https://doi.org/10.1007/978-1-4020-8506-2_1)

908 Hollinger, D.Y., Aber, J., Dail, B., Davidson, E.A., Goltz, S.M., Hughes, H., Leclerc,  
909 M.Y., Lee, J.T., Richardson, A.D., Rodrigues, C., Scott, N. a., Achuatavariet, D.,  
910 Walsh, J., 2004. Spatial and temporal variability in forest–atmosphere CO<sub>2</sub>  
911 exchange. *Glob. Change Biol.* 10, 1689–1706. <https://doi.org/10.1111/j.1365-2486.2004.00847.x>

912

913 Hu, J., Moore, D.J.P., Burns, S.P., Monson, R.K., 2010. Longer growing seasons lead to  
914 less carbon sequestration by a subalpine forest. *Glob. Change Biol.* 16, 771–783.  
915 <https://doi.org/10.1111/j.1365-2486.2009.01967.x>

916 Hui, D., Luo, Y., Katul, G., 2003. Partitioning inter annual variability in net ecosystem  
917 exchange between climatic variability and functional change. *Tree Physiol.* 23,  
918 433–442.

919 Keith, H., Wong, S.C., 2006. Measurement of soil CO<sub>2</sub> efflux using soda lime  
920 absorption: both quantitative and reliable. *Soil Biol. Biochem.* 38, 1121–1131.  
921 <https://doi.org/10.1016/j.soilbio.2005.09.012>

922 Körner, C., 2015. Paradigm shift in plant growth control. *Curr. Opin. Plant Biol.* 25, 107–  
923 114. <https://doi.org/10.1016/j.pbi.2015.05.003>

924 Körner, C., 2003. Carbon limitation in trees. *J. Ecol.* 91, 4–17.  
925 <https://doi.org/10.1046/j.1365-2745.2003.00742.x>

926 Litton, C.M., Raich, J.W., Ryan, M.G., 2007. Carbon allocation in forest ecosystems.  
927 *Glob. Change Biol.* 13, 2089–2109. <https://doi.org/10.1111/j.1365-2486.2007.01420.x>

928

929 Luysaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais,  
930 P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–  
931 215. <https://doi.org/10.1038/nature07276>

932 Matzner, E., Borken, W., 2008. Do freeze-thaw events enhance C and N losses from soils  
933 of different ecosystems? A review. *Eur. J. Soil Sci.* 59, 274–284.  
934 <https://doi.org/10.1111/j.1365-2389.2007.00992.x>

935 McFarlane, K., Finzi, A., Nave, L., Tang, J., 2014. Recommendations for belowground  
936 carbon data and measurements for the AmeriFlux Network [WWW Document].  
937 ISCN. URL <http://iscn.fluxdata.org/community/publication/recommendations-for->

938 belowground-carbon-data-and-measurements-for-the-ameriflux-network/  
939 (accessed 4.18.17).

940 Novick, K., Brantley, S., Miniati, C.F., Walker, J., Vose, J.M., 2014. Inferring the  
941 contribution of advection to total ecosystem scalar fluxes over a tall forest in  
942 complex terrain. *Agric. For. Meteorol.* 185, 1–13.  
943 <https://doi.org/10.1016/j.agrformet.2013.10.010>

944 Odum, E.P., 1969. The Strategy of Ecosystem Development. *Science* 164, 262–270.  
945 <https://doi.org/10.1126/science.164.3877.262>

946 Ollinger, S.V., Smith, M.L., Martin, M.E., Hallett, R.A., Goodale, C.L., Aber, J.D., 2002.  
947 Regional Variation in Foliar Chemistry and N Cycling among Forests of Diverse  
948 History and Composition. *Ecology* 83, 339–355. <https://doi.org/10.2307/2680018>

949 Ouimette, A., Guo, D., Hobbie, E., Gu, J., 2013. Insights into root growth, function, and  
950 mycorrhizal abundance from chemical and isotopic data across root orders. *Plant  
951 Soil* 367, 313–326. <https://doi.org/10.1007/s11104-012-1464-4>

952 Park, B.B., Yanai, R.D., Vadeboncoeur, M.A., Hamburg, S.P., 2007. Estimating Root  
953 Biomass in Rocky Soils using Pits, Cores, and Allometric Equations. *Soil Sci.  
954 Soc. Am. J.* 71, 206–213. <https://doi.org/10.2136/sssaj2005.0329>

955 Pesonen, A., Leino, O., Maltamo, M., Kangas, A., 2009. Comparison of field sampling  
956 methods for assessing coarse woody debris and use of airborne laser scanning as  
957 auxiliary information. *For. Ecol. Manag.* 257, 1532–1541.  
958 <https://doi.org/10.1016/j.foreco.2009.01.009>

959 Phillips, C.L., Bond-Lamberty, B., Desai, A.R., Lavoie, M., Risk, D., Tang, J., Todd-  
960 Brown, K., Vargas, R., 2017. The value of soil respiration measurements for  
961 interpreting and modeling terrestrial carbon cycling. *Plant Soil* 413, 1–25.  
962 <https://doi.org/10.1007/s11104-016-3084-x>

963 Phillips, S.C., Varner, R.K., Frothingham, S., Munger, J.W., Bubier, J.L., Wofsy, S.C., Crill,  
964 P.M., 2010. Interannual, seasonal, and diel variation in soil respiration relative to  
965 ecosystem respiration at a wetland to upland slope at Harvard Forest. *J. Geophys.  
966 Res. Biogeosciences* 115, G02019. <https://doi.org/10.1029/2008JG000858>

967 Post, W.M., Kwon, K.C., 2000. Soil carbon sequestration and land-use change: processes  
968 and potential. *Glob. Change Biol.* 6, 317–327. <https://doi.org/10.1046/j.1365-2486.2000.00308.x>

970 Potter, D., Obbard, M., Howe, E., 2015. Ontario wildlife food survey, 2014. Ont. Minist.  
971 Nat. Resour. For. Sci. Res. Branch Peterb. Ont. Sci. Res. Tech. Rep. TR-01.

972 Raich, J.W., Nadelhoffer, K.J., 1989. Belowground Carbon Allocation in Forest  
973 Ecosystems: Global Trends. *Ecology* 70, 1346–1354.  
974 <https://doi.org/10.2307/1938194>

975 Richardson, A.D., Braswell, B.H., Hollinger, D.Y., Burman, P., Davidson, E.A., Evans,  
976 R.S., Flanagan, L.B., Munger, J.W., Savage, K., Urbanski, S.P., Wofsy, S.C.,  
977 2006. Comparing simple respiration models for eddy flux and dynamic chamber  
978 data. *Agric. For. Meteorol.* 141, 219–234.  
979 <https://doi.org/10.1016/j.agrformet.2006.10.010>

980 Richardson, A.D., Carbone, M.S., Keenan, T.F., Czimczik, C.I., Hollinger, D.Y.,  
981 Murakami, P., Schaberg, P.G., Xu, X., 2013. Seasonal dynamics and age of  
982 stemwood nonstructural carbohydrates in temperate forest trees. *New Phytol.* 197,  
983 850–861. <https://doi.org/10.1111/nph.12042>

984 Richardson, A.D., Hollinger, D.Y., 2007. A method to estimate the additional uncertainty  
985 in gap-filled NEE resulting from long gaps in the CO<sub>2</sub> flux record. *Agric. For.*  
986 *Meteorol.* 147, 199–208. <https://doi.org/10.1016/j.agrformet.2007.06.004>

987 Richardson, A.D., Hollinger, D.Y., Aber, J.D., Ollinger, S.V., Braswell, B.H., 2007.  
988 Environmental variation is directly responsible for short- but not long-term  
989 variation in forest-atmosphere carbon exchange. *Glob. Change Biol.* 13, 788–803.  
990 <https://doi.org/10.1111/j.1365-2486.2007.01330.x>

991 Russell, M.B., Woodall, C.W., Fraver, S., D’Amato, A.W., Domke, G.M., Skog, K.E.,  
992 2014. Residence Times and Decay Rates of Downed Woody Debris  
993 Biomass/Carbon in Eastern US Forests. *Ecosystems* 17, 765–777.  
994 <https://doi.org/10.1007/s10021-014-9757-5>

995 Smith, M.-L., Hollinger, D.Y., Ollinger, S., 2008. Estimation of Forest Canopy Nitrogen  
996 Concentration, in: Hoover, C.M. (Ed.), *Field Measurements for Forest Carbon*  
997 *Monitoring*. Springer Netherlands, pp. 197–203. [https://doi.org/10.1007/978-1-4020-8506-2\\_15](https://doi.org/10.1007/978-1-4020-8506-2_15)

998  
999 Song, Y., Zou, Y., Wang, G., Yu, X., 2017. Altered soil carbon and nitrogen cycles due  
1000 to the freeze-thaw effect: A meta-analysis. *Soil Biol. Biochem.* 109, 35–49.  
1001 <https://doi.org/10.1016/j.soilbio.2017.01.020>

1002 Thomas, S.C., Martin, A.R., 2012. Carbon Content of Tree Tissues: A Synthesis. *Forests*  
1003 3, 332–352. <https://doi.org/10.3390/f3020332>

1004 Tjoelker, M.G., Oleksyn, J., Reich, P.B., 2001. Modelling respiration of vegetation:  
1005 evidence for a general temperature-dependent Q<sub>10</sub>. *Glob. Change Biol.* 7, 223–  
1006 230. <https://doi.org/10.1046/j.1365-2486.2001.00397.x>

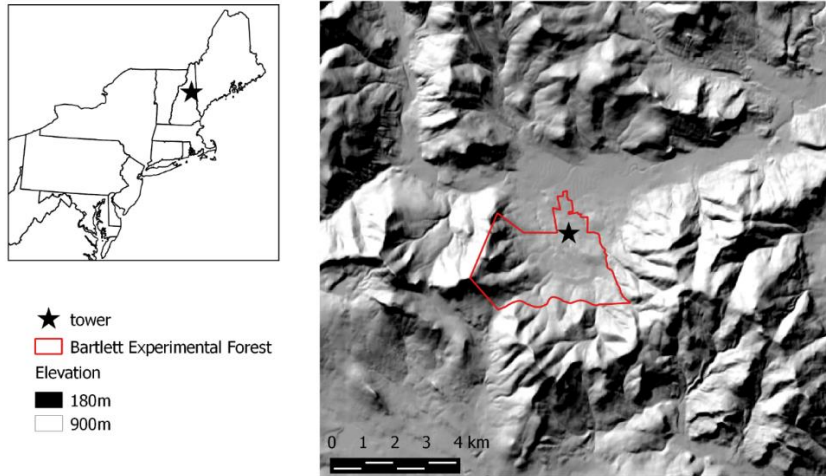
1007 Vadeboncoeur, M.A., Hamburg, S.P., Blum, J.D., Pennino, M.J., Yanai, R.D., Johnson,  
1008 C.E., 2012. The Quantitative Soil Pit Method for Measuring Belowground Carbon  
1009 and Nitrogen Stocks. *Soil Sci. Soc. Am. J.* 76, 2241–2255.  
1010 <https://doi.org/10.2136/sssaj2012.0111>

1011 Vadeboncoeur, M.A., Hamburg, S.P., Yanai, R.D., Blum, J.D., 2014. Rates of sustainable  
1012 forest harvest depend on rotation length and weathering of soil minerals. *For.*  
1013 *Ecol. Manag. Complete*, 194–205. <https://doi.org/10.1016/j.foreco.2014.01.012>

1014 Valentine, H.T., Gove, J.H., Ducey, M.J., Gregoire, T.G., Williams, M.S., 2008.  
1015 Estimating the Carbon in Coarse Woody Debris with Perpendicular Distance  
1016 Sampling, in: Hoover, C.M. (Ed.), *Field Measurements for Forest Carbon*  
1017 *Monitoring*. Springer Netherlands, pp. 73–87. [https://doi.org/10.1007/978-1-4020-8506-2\\_6](https://doi.org/10.1007/978-1-4020-8506-2_6)

1018  
1019 van Gorsel, E., Delpierre, N., Leuning, R., Black, A., Munger, J.W., Wofsy, S., Aubinet,  
1020 M., Feigenwinter, C., Beringer, J., Bonal, D., Chen, B., Chen, J., Clement, R.,  
1021 Davis, K.J., Desai, A.R., Dragoni, D., Etzold, S., Grünwald, T., Gu, L., Heinesch,  
1022 B., Hutryra, L.R., Jans, W.W.P., Kutsch, W., Law, B.E., Leclerc, M.Y.,  
1023 Mammarella, I., Montagnani, L., Noormets, A., Rebmann, C., Wharton, S., 2009.  
1024 Estimating nocturnal ecosystem respiration from the vertical turbulent flux and  
1025 change in storage of CO<sub>2</sub>. *Agric. For. Meteorol., Special Section on Water and*  
1026 *Carbon Dynamics in Selected Ecosystems in China* 149, 1919–1930.  
1027 <https://doi.org/10.1016/j.agrformet.2009.06.020>

1028 Vickers, D., Irvine, J., Martin, J.G., Law, B.E., 2012. Nocturnal subcanopy flow regimes  
1029 and missing carbon dioxide. *Agric. For. Meteorol.* 152, 101–108.  
1030 <https://doi.org/10.1016/j.agrformet.2011.09.004>  
1031 Whittaker, R.H., Bormann, F.H., Likens, G.E., Siccama, T.G., 1974. The Hubbard Brook  
1032 Ecosystem Study: Forest Biomass and Production. *Ecol. Monogr.* 44, 233–254.  
1033 <https://doi.org/10.2307/1942313>  
1034 Yanai, R.D., Battles, J.J., Richardson, A.D., Blodgett, C.A., Wood, D.M., Rastetter, E.B.,  
1035 2010. Estimating Uncertainty in Ecosystem Budget Calculations. *Ecosystems* 13,  
1036 239–248. <https://doi.org/10.1007/s10021-010-9315-8>  
1037 Yanai, R.D., Vadeboncoeur, M.A., Hamburg, S.P., Arthur, M.A., Fuss, C.B., Groffman,  
1038 P.M., Siccama, T.G., Driscoll, C.T., 2013. From Missing Source to Missing Sink:  
1039 Long-Term Changes in the Nitrogen Budget of a Northern Hardwood Forest.  
1040 *Environ. Sci. Technol.* 47, 11440–11448. <https://doi.org/10.1021/es4025723>  
1041 Young, H.E., Ribe, J.H., Wainwright, K., 1980. Weight tables for tree and shrub species  
1042 in Maine. *Maine Life Sci. Agric. Exp. Stn. Misc. Rep. USA.*  
1043  
1044



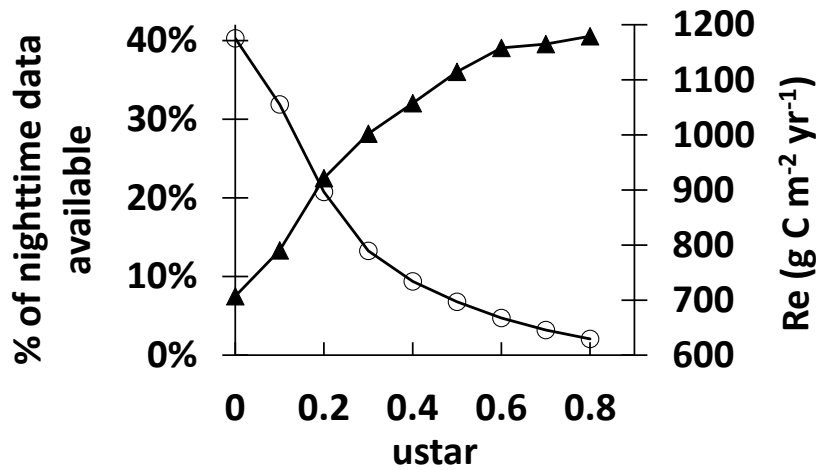
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1046 **Figure 1: A) Location of Bartlett Experimental Forest (BEF); B) Representation of topography**  
 1047 **surrounding BEF.**

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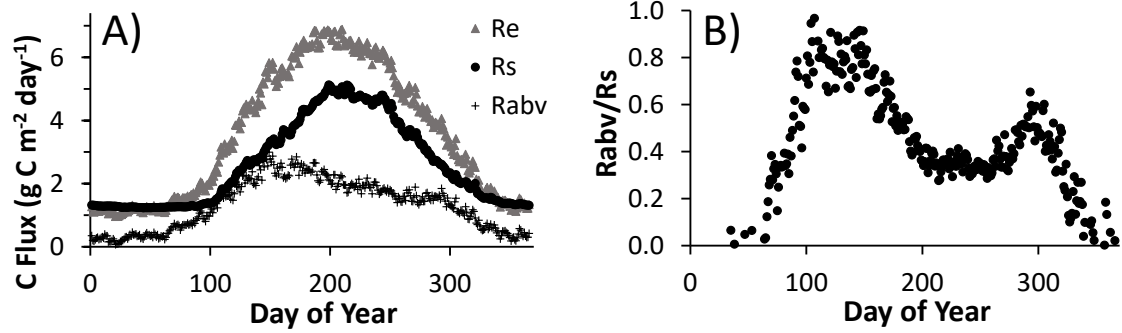


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1052 **Figure 2: Plot of the percent of available nighttime data during the growing season (circles) and**  
 1053 **mean annual ecosystem respiration (triangles) with changes in ustar, highlighting the tradeoff**  
 1054 **between data quantity and data quality at BEF.**

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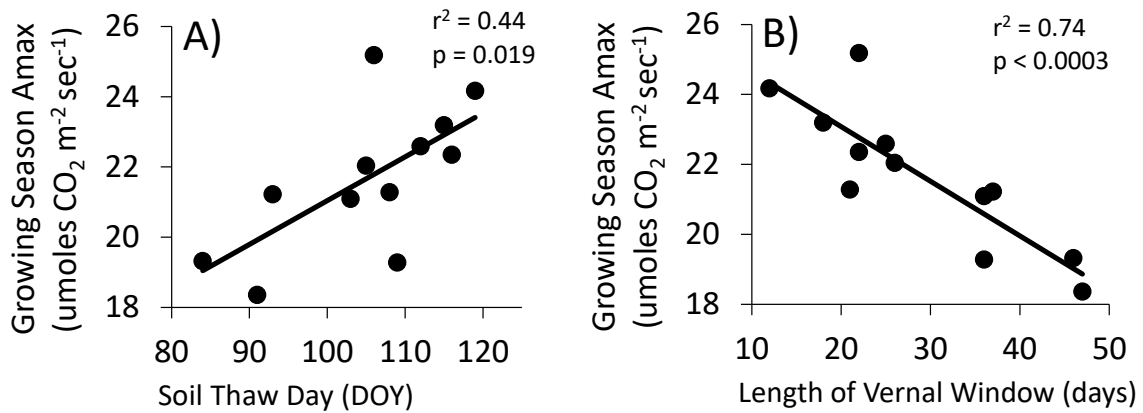
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1058 **Figure 3: A) Mean daily CO<sub>2</sub> flux by day of year for ecosystem respiration (Re<sub>EC</sub>), soil respiration**  
 1059 **(Rs), and respiration from aboveground components of the ecosystem (R<sub>abv</sub>); B) Ratio of R<sub>abv</sub> to Rs**  
 1060 **by day of year.**

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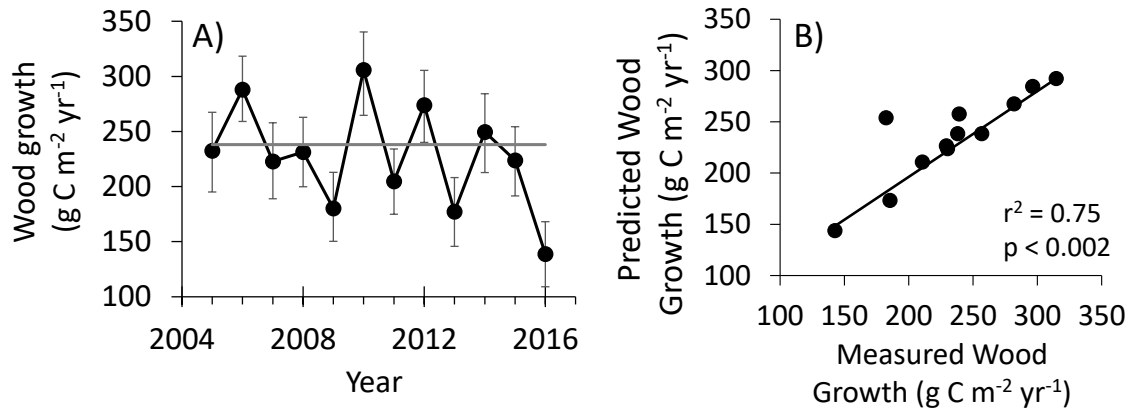
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1065 **Figure 4: Relationship between growing season canopy level Amax and (A) soil thaw day, and (B) the**  
 1066 **length of the vernal window during 2004-2016. The vernal window is defined as the number of days**  
 1067 **between soil thaw and the start of canopy gross carbon uptake.**

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1070 **Figure 5: A) Annual wood growth during 2004-2016 including both aboveground biomass and coarse**  
 1071 **roots. B) Predicted vs. measured wood growth. Predicted wood growth was estimated from a 2**  
 1072 **parameter linear regression model using early summer air temperature (Julian days 136-215) and a**  
 1073 **drought index (the number of growing season days with VWC < 17.5%; 50% of the growing season**  
 1074 **mean VWC). The outlier in B) is 2013 where measured wood growth was much lower than**  
 1075 **predicted.**

1076



**Table 1: Mean carbon fluxes and uncertainty at Bartlett Experimental Forest, NH (2004-2016)**

<b>Components of Net Primary Production</b>		
	Flux ( $\text{g C m}^{-2} \text{ yr}^{-1}$ )	Method
(a) Aboveground Wood	$204 \pm 29$	(1 + 2 + 3)
1) Large trees (>12.7 cm dbh)	$143 \pm 20$	Allometry; annual DBH
2) Small trees (<12.7 cm dbh)	$30 \pm 5$	Allometry; annual DBH
3) branchfall	$31 \pm 21$	Annual branchfall tarps
(b) Foliage, fruit, flower	$123 \pm 11$	Annual litterfall collection
(c) Understory/herbivory	$20 \pm 10$	Allometry on microplots
(d) Woody roots	$34 \pm 7$	Allometry; annual DBH
(e) Fine roots	$110 \pm 64$	Root ingrowth cores
(f) Mycorrhizae	$124 \pm 93$	Stable isotope approach
(h) Total NPP	$615 \pm 118$	(a + b + c + d + e + f)

**Respiratory Fluxes**

(i) Total Soil Respiration ( $R_S$ )	$810 \pm 48$	Manual and auto-chambers
(j) CWD respiration	$5 \pm 5$	CWD mass; mass loss rates
(k) Standing dead respiration	$56 \pm 15$	Allometry; mass loss rates
(l) Woody autotrophic respiration	$153 \pm 114$	$0.118 * \text{GPP}_B$ ; see methods
(m) Foliar respiration	$149 \pm 20$	leaf level measurements
(n) Heterotrophic Soil Respiration ( $R_{SH}$ )	$434 \pm 101$	$1.92 + 0.534 * (i)$ ; see methods
(o) Autotrophic Soil respiration ( $R_{SA}$ )	$376 \pm 101$	1 - (n)

**Ecosystem Fluxes**

$\text{NEP}_{EC}$	$132 \pm 49$	eddy covariance flux tower (-NEE)
$\text{NEP}_B$	$120 \pm 156$	$\text{NPP} - R_B$ ; (h - j - k - n)
$\Delta C$	$133 \pm 34$	modified inventory approach
$\text{Re}_{EC}$	$1153 \pm 69$	eddy covariance flux tower
$\text{Re}_B$	$1172 \pm 127$	(i + j + k + l + m)
$\text{GPP}_{EC}$	$1285 \pm 62$	eddy covariance flux tower
$\text{GPP}_B$	$1292 \pm 194$	(h + l + m + o)
TBCA	$656 \pm 54$	(i - b - 3)