

Coupling of Tree Growth and Photosynthetic Carbon Uptake Across Six North American Forests

Key Points:

- We found evidence for lags in allocation of previous year's carbon uptake to wood biomass increment (WBI) at three of six sites studied
- Sites with high annual WBI demonstrated strong correlations to carbon uptake, with the strongest correlations including previous year uptake
- WBI was less tightly coupled to carbon uptake in less productive forests that also exhibited low interannual variability in WBI

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:

Teets, A., Moore, D. J. P., Alexander, M. R., Blanken, P. D., Bohrer, G., Burns, S. P., et al. (2022). Coupling of tree growth and photosynthetic carbon uptake across six North American forests. *Journal of Geophysical Research: Biogeosciences*, 127, e2021JG006690. <https://doi.org/10.1029/2021JG006690>

Received 28 OCT 2021
Accepted 14 MAR 2022

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Abstract Linking biometric measurements of stand-level biomass growth to tower-based measurements of carbon uptake—gross primary productivity and net ecosystem productivity—has been the focus of numerous ecosystem-level studies aimed to better understand the factors regulating carbon allocation to slow-turnover wood biomass pools. However, few of these studies have investigated the importance of previous year uptake to growth. We tested the relationship between wood biomass increment (WBI) and different temporal periods of carbon uptake from the current and previous years to investigate the potential lagged allocation of fixed carbon to growth among six mature, temperate forests. We found WBI was strongly correlated to carbon uptake across space (i.e., long-term averages at the different sites) but on annual timescales, WBI was much less related to carbon uptake, suggesting a temporal mismatch between C fixation and allocation to biomass. We detected lags in allocation of the previous year's carbon uptake to WBI at three of the six sites. Sites with higher annual WBI had overall stronger correlations to carbon uptake, with the strongest correlations to carbon uptake from the previous year. Only one site had WBI with strong positive relationships to current year uptake and not the previous year. Forests with low rates of WBI demonstrated weak correlations to carbon uptake from the previous year and stronger relationships to current year climate conditions. Our work shows an important, but not universal, role of lagged allocation of the previous year's carbon uptake to growth in temperate forests.

Plain Language Summary We compared the interannual variability of stand-level biomass growth (estimated from annual tree-level measurements) to carbon uptake (measured from towers monitoring gas exchange over forest canopies) to identify temporal mismatches between the two processes. We used data from multiple forested sites with long-term measurements of carbon uptake to ask the question: is there a consistent temporal offset between the uptake of carbon and the allocation to plant biomass? We found that the relationship between growth and carbon uptake varies among sites, and there was no consistent temporal offset between the uptake of carbon and allocation to biomass growth. Sites with higher growth rates had higher interannual variability, and more apparent coupling between biomass growth and carbon uptake from the previous year. Forests with lower growth rates had weaker relationships with carbon uptake and stronger coupling with current year environmental conditions. We demonstrate that temporal lags between carbon uptake and allocation to growth are not universal among these temperate forests, and the carry-over of uptake stored from the previous year is not as critical in slow-growing forests, compared to fast-growing forests, likely due

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to lower demands for growth. This work helps to clarify the limitations on the growth of slow-turnover wood biomass.

1. Introduction

Biomass stored in trees represents the largest pool of living carbon on the planet (Houghton et al., 2009), and the growth of new tree tissues is one of the largest and most persistent global sinks of atmospheric carbon (Pan et al., 2011). Once carbon is allocated to structural growth in trees, as lignin or cellulose, it becomes relatively recalcitrant (Alexander et al., 2018; Russell et al., 2014) and provides the foundation for long-term carbon sequestration in forests. Direct measurements of tree growth are commonly used to estimate the rates of carbon moving into forest ecosystems. Tree rings (Babst et al., 2014; Bouriaud et al., 2005) or repeated annual biometric inventories (Clark et al., 2001) combined with allometric equations are used to quantify whole forest wood biomass increment (WBI) with annual resolution. We refer to WBI as the stand-level mass of carbon allocated to boles, branches, and coarse roots of trees annually. Long-time series of WBI are useful for several different applications, including carbon accounting purposes (e.g., Hollinger et al., 2021), reconciling ecosystem models (Xu et al., 2017), and monitoring forest carbon accumulation in forest ecosystems through time.

Despite the importance of wood biomass production to the global carbon cycle, the environmental controls on the interannual variability of WBI remain only partially understood. This is largely because we do not understand how WBI is related to the source of carbon needed for growth—photosynthetic carbon uptake (Sala et al., 2012). At the ecosystem level, metrics of carbon uptake (i.e., net ecosystem productivity [NEP] and gross primary productivity [GPP]) are measured from towers using high-frequency observations of the covariance between the vertical wind speed and atmospheric CO₂ concentration (Baldocchi et al., 1988). While multiyear averages of WBI are considered highly correlated with multiyear averages of NEP (Pregitzer & Euskirchen, 2004) and GPP (Waring et al., 1998; Zha et al., 2013), the interannual variability of these metrics are oftentimes decoupled from one another (e.g., Delpierre et al., 2016). Understanding the relationship between WBI and carbon uptake is a critical step in understanding the environmental controls on WBI.

In the last two decades, researchers have tested the relationship between WBI and annual carbon uptake (measured from eddy covariance towers) across several different forest types to better understand the limitations on stand-level biomass growth (e.g., Babst et al., 2013). While some studies have found strong relationships between the interannual variability of WBI and annual carbon uptake (e.g., Lempereur et al., 2015; Ohtsuka et al., 2009), others have found carbon uptake over calendar-year timescales to be largely decoupled from WBI (e.g., Barford et al., 2001; Curtis et al., 2002; Teets et al., 2018). Some studies found subannual integrals of carbon uptake are better predictors of WBI (Babst et al., 2013; Gea-Izquierdo et al., 2014; Granier et al., 2008) because they have the benefit of excluding winter seasons when temperate trees are not actively photosynthesizing. Despite the growing amount literature on this topic (also see Anić et al., 2018; Guillemot et al., 2015; Rocha et al., 2006), it is difficult to synthesize this information due to (a) different metrics and analytical approaches used to characterize relationships between WBI and carbon uptake, (b) different forest types studied, and (c) varying climatology affecting trees where the studies are located. In addition, these studies rarely test the relationship between WBI and carbon uptake from the previous year.

It is possible that weak correlations found between stand-level growth and carbon uptake in many of these studies are due to delays in carbon allocation (i.e., lags) until growth the following year (see Gough et al., 2009; Richardson et al., 2013). Lags in allocation are commonly associated with negative conditions for WBI—when stressful conditions (e.g., droughts) can cause negative growth effects lasting for several years (Anderegg et al., 2015; Kannenberg et al., 2020; Ogle et al., 2015). But lags in allocation of carbon to structural growth can also occur under normal environmental conditions. When carbon uptake exceeds the demand for growth surplus photosynthate is allocated to storage as nonstructural carbohydrates (Hartmann et al., 2015; Kozłowski, 1992). Allocation of previously stored nonstructural carbohydrates to growth in following years has been demonstrated using isotopic tracers (e.g., Epron et al., 2012; Keel et al., 2006; Mildner et al., 2014) and delayed allocation of carbohydrates is thought to be largely responsible for autocorrelation found in tree-ring widths (Carbone et al., 2013; Kagawa et al., 2006). Although delayed responses of past year's conditions on tree growth has been recognized by dendrochronologists for several decades (e.g., Fritts, 1976), we still do not understand the mechanisms explaining different lagged growth responses between species (Zweifel & Sterck, 2018) and forest types.

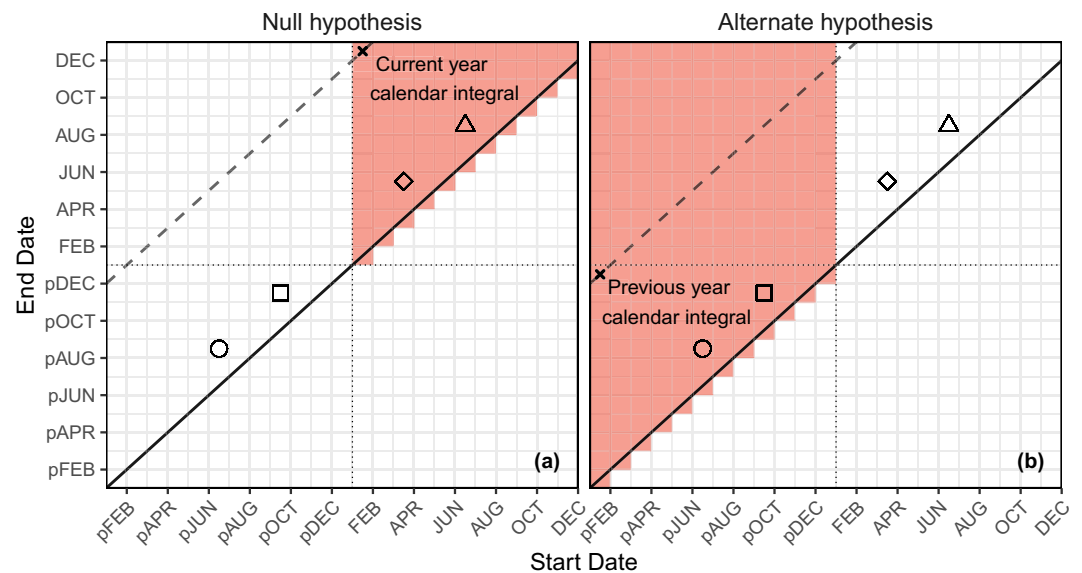


Figure 1. Conceptual diagram of correlation matrices used in this study. Each 1×1 quadrant represents a variable integrated over a different temporal period (start of integral on x-axis, and end of integral on y-axis). The x- and y-axes origin represents January of the year before growth (the prefix *p* refers to previous years). The 1-to-1 line (solid line) represents 1-month integrals, the shortest temporal period used for this study. The dashed line represents 12-month integrals (the area above the line represents temporal periods >1 year, and the area below the line is less than 1 year). The dotted lines separate the two calendar years. The lower left quadrant represents only previous year metrics, the top right quadrant current year integrals, and the top left including portions of both current and previous year metrics. Shape outlines refer to different seasons: previous year summer (O), previous year autumn (\square), spring (\diamond), and summer (\triangle) uptake.

Lagged allocation of carbon can also occur due to seasonal differences between growth and photosynthesis. Compared to photosynthesis, growth of new wood tissues in cold-climate temperate forests occurs over relatively short temporal periods in the late spring and summer (D'Orangeville et al., 2021; Rossi et al., 2006) because xylogenesis (i.e., wood formation) is more sensitive to low temperatures (Körner, 1998) and moisture deficits (Estiarte & Penuelas, 1999; Kozłowski & Pallardy, 2002) than is photosynthesis. In temperate forests, reserves of sugars and starch (i.e., nonstructural carbohydrates) accumulate once growth has completed and are typically highest just before winter dormancy (Furze et al., 2018). At times, it is thought that growth is actively downregulated to allow the accumulation of nonstructural carbohydrates (Dietze et al., 2014). When favorable conditions return, trees can remobilize stored carbohydrates from the previous year to initiate growth in the spring (Eglin et al., 2010; Kuptz et al., 2011). Documenting lagged allocation of carbon stand-level growth would validate the importance of lagged growth responses at the ecosystem scale and has rarely been tested (but see Gough et al., 2009).

In this study, we test whether temporal lags in carbon allocation to stand-level growth are found across six different North American forests. We ask, is annual WBI better explained by carbon uptake (i.e., NEP and GPP) from the previous year (i.e., lags in allocation) compared to current year carbon uptake? We explore the research question systematically at multiple sites to test whether the temporal relationship between WBI and carbon uptake is conserved or varies among forests. Our null hypothesis was that WBI exhibits significant positive correlations to only current year carbon uptake among forests, suggesting little reliance on previously stored carbohydrates for growth. Our alternate hypothesis was that WBI, across all sites studied, exhibits strong positive correlations with carbon uptake integrals from the previous year, suggesting there are consistent and measurable lags in the allocation of stored nonstructural carbohydrates for later growth. To test these hypotheses, we identified the periods of carbon uptake most strongly correlated to WBI using a correlation matrix approach (as used in Babst et al., 2013) to characterize the relationships between WBI and different temporal periods of carbon uptake at the different sites (see conceptual figure of the hypotheses in Figure 1). Following, we tested whether WBI responds to current or previous year climate drivers using the same methodology. By identifying the drivers of WBI, we can better understand the factors that regulate the stand-level growth of long-lived wood biomass, an important process that

Table 1

Site and Data Description for AmeriFlux Sites Listed by Increasing Mean Annual Temperature (and Decreasing Conifer Cover) From Left to Right

	Niwot Ridge	Howland Forest	Bartlett Experimental Forest	University of Michigan Biological Station	Harvard Forest	Morgan Monroe State Forest
Site ID	US-NR1	US-Ho1	US-Bar	US-UMB	US-Ha1	US-MMS
Location	Colorado, U.S.	Maine, U.S.	New Hampshire, U.S.	Michigan, U.S.	Massachusetts, U.S.	Indiana, U.S.
Mean annual temperature (°C)	1.5	5.3	5.6	5.8	6.6	10.9
Mean annual precipitation (mm)	800	1,070	1,246	803	1,071	1,032
Elevation (m)	3,050	60	272	234	340	275
Dominant genera in decreasing order	<i>Abies</i> , <i>Pinus</i> , and <i>Picea</i>	<i>Picea</i> and <i>Tsuga</i>	<i>Acer</i> , <i>Fagus</i> , and <i>Betula</i>	<i>Populus</i> , <i>Quercus</i> , and <i>Pinus</i>	<i>Quercus</i> and <i>Acer</i>	<i>Liriodendron</i> , <i>Acer</i> , and <i>Quercus</i>
EPA ^a Ecoregion Level III	Southern Rockies	Acadian Plains and Hills	Northeastern Highlands	Northern Lakes and Forests	Northeastern Highlands	Eastern Temperate Forests
QMD ^b (cm) in 2012	19	29	26	24	37	44
Living tree biomass ^c in 2012 (Mg C ha ⁻¹ ± SD)	46 ± 11	138 ± 18	96 ± 16	64 ± 12	153 ± 34	121 ± 39
Leaf area index (m ² m ⁻²) ^d	3.8–4.2	5.3–6.3	4.0–5.5	3.4–4.4	4.5–5.5	4.2–5.2
References	Burns et al. (2015); Monson et al. (2005)	Hollinger et al. (2004)	Ouimette et al. (2018)	Gough et al. (2013)	Urbanski et al. (2007)	Schmid et al. (2000)
Data set DOI	Blanken et al. (1998; 10.17190/AMF/12460880)	Hollinger (1996; 10.17190/AMF/1246061)	Richardson (2004; 10.17190/AMF/1246030)	Gough et al. (1999; 10.17190/AMF/1246107)	Munger (1991; 10.17190/AMF/1246059)	Novick and Phillips (1999; 10.17190/AMF/1246080)

^aEPA = U.S. Environmental Protection Agency. ^bQMD = quadratic mean diameter of the trees sampled. ^cUncertainty calculated from Monte Carlo sampling with replacement of individual tree biomass. ^dLAI was estimated from harvesting trees and scaling to the stand level at US-NR1 (Turnipseed et al., 2002), litter collection at US-UMB, and using the LAI 2000 plant canopy analyzer (Li-Cor Inc, Lincoln, NE) at US-Ho1, US-Bar, US-Ha1, and US-MMS.

remains only partially understood (Dietze et al., 2014). Characterizing the link between WBI and carbon uptake is therefore an important step in understanding forest carbon cycling.

2. Materials and Methods

2.1. Description of Data Sources

We compiled a data set of previously collected biometric measurements of WBI to compare with the eddy covariance data from six temperate forests (described in Table 1) within the AmeriFlux network (ameriflux.lbl.gov). We selected temperate forest sites with greater than 10 years of continuous eddy covariance measurements to ensure the time series were sufficiently long to assess the relationship between the two approaches. The sites are mature forests that are representative of mid-to late-successional secondary forest types for each region, including three in the northeastern United States (Howland Forest, US-Ho1; Bartlett Experimental Forest, US-Bar; and Harvard Forest, US-Ha1), two in the midwestern United States (University of Michigan Biological Station, US-UMB; and Morgan Monroe State Forest, US-MMS), and one high elevation forest site in the Rocky Mountain region of the United States (Niwot Ridge, US-NR1). These forests vary in climate, species composition, and standing biomass (Table 1). Throughout the remainder of the manuscript, the sites will be referred to by their AmeriFlux site identifiers (IDs).

2.1.1. Wood Biomass Increment

Annual WBI was estimated for individual trees by reconstructing time series of tree diameter, and then using allometric equations to estimate the change in whole tree biomass over time. Diameter time series was developed from repeated annual measurements at US-Bar (2005–2017), and from increment cores at the remaining five sites, collected between 2012 and 2015 (see Alexander, 2017; Dye et al., 2019; Teets et al., 2018). Trees were selected based on randomly allocated plots located within the eddy covariance tower footprint, with a 10 cm (at breast height) minimum diameter of sampled trees. Data were collected by different researchers at different times, and sampling protocols varied among some of the sites. As a result, our sites had varying plot designs, areas sampled, and number of trees sampled (Table S1 in Supporting Information S1).

To allow for unbiased comparison between measurements among sites, we standardized processing of tree measurement data to annual WBI reported per unit land area. Annual tree-ring measurements were used to sequentially back-calculate tree diameters since tower establishment. First, we estimated inside bark diameters of sampled trees using region-specific and species-specific bark factors (Dixon & Keyser, 2011, 2013; Keyser & Dixon, 2008), then subtracted two times the measured tree-ring width (doubling a radial measurement to calculate diameter change), then used bark factors to calculate the outside bark diameter for each year. Aboveground dry tree biomass was then estimated for each year using genus-specific or family-specific allometric equations (Chojnacky et al., 2014). These equations have the benefit of using consistent equation structures, inputs (all diameter-based equations), outputs (whole-tree aboveground dry-weight biomass), and units (centimeter diameter inputs and kilogram outputs) for all the sites. Belowground biomass was also estimated from Chojnacky et al. (2014) equations and added to aboveground biomass to yield whole-tree dry biomass. These belowground estimates assume consistent root:shoot ratios (approximately 1:5) across sites because we do not have site-level data needed for accurate estimates of belowground biomass. We use these genus-level or family-level equations because regionally developed equations were not available for all species at all sites, and different equation structures can cause bias among species. Whole tree (above-ground and below-ground) biomass increment was then converted to carbon biomass increment by multiplying by the standard carbon fraction of 0.5, which is a reasonable estimate for temperate angiosperm and conifer tree species (Thomas & Martin, 2012). WBI from individual trees were then summed at the plot level and converted to grams of carbon per square meter per year ($\text{g C m}^{-2} \text{yr}^{-1}$).

Using diameter growth has become a standard approach to estimate changes in tree-level and stand-level biomass accumulation (see Foster et al., 2016). But estimating tree-level biomass increment from diameter growth requires the assumption that whole-tree biomass change is proportional to the change in diameter (Bouriaud et al., 2005). This can introduce uncertainties from annual variability in height growth, root growth, and reproductive effort that are not captured in diameter measurements (Mund et al., 2020). Variability in wood density is another source of uncertainty that affects the accuracy of annual tree-level biomass estimation (Babst et al., 2013) by as much as 30% in some hardwood forests (Delpierre et al., 2016). Additional assumptions are then required when scaling up from tree-level to stand-level estimates of biomass growth. Stand-level WBI estimated from trees does not account for growth of understory plants and saplings. Understory plants account for larger proportions of ecosystem carbon uptake in forests with open canopies compared to dense forests with little light penetration (in this study all of our sites had closed canopies). Predicting WBI back in time also does not account for growth of trees that died prior to sampling (Foster et al., 2014), an assumption that becomes more problematic over long time series. When comparing WBI time series to NEP, carbon sources like decomposition and soil respiration can affect the results because they are largely unrelated to tree carbon balance. Comparisons between WBI and GPP are thought to be more analogous, but unlike NEP, these values are modeled from the data (Desai et al., 2008), and are not measured directly. Despite these several sources of uncertainty, WBI estimated from tree-level measurements is considered a reliable proxy for net primary productivity (Xu et al., 2017).

We also make the assumption that our randomly allocated biometric plots are representative of the footprint of the eddy covariance system. We assessed how tree sampling affected the uncertainty of WBI by conducting Monte Carlo simulations of the sampled trees. For each forest plot, we selected a random sample with replacement of individual trees and assigned them to 1,000 artificial plots with the number of trees based on a Poisson distribution around the average number of trees per plot. For each simulation, we calculated the time series of plot-level WBI by summing the tree-level biomass growth at each yearly timestep. Because we were primarily interested in the uncertainty of the annual variability, and only secondarily interested in the uncertainty in the magnitude

of WBI, we calculated annual uncertainty as the standard deviation of the difference between the yearly WBI and the simulation mean. This is different from the uncertainty in the total magnitude of WBI, because it is the uncertainty in the deviation of each year's measurement to the mean. This uncertainty was estimated to determine how reliably we could detect interannual patterns of WBI. It is important to evaluate the sampling uncertainty because individual trees and species can respond differently to environmental conditions.

2.1.2. Carbon Uptake

At each site, carbon uptake was quantified by measuring CO₂ exchange above the forest canopy using the eddy covariance technique (Baldocchi et al., 1988). The eddy covariance technique measures net ecosystem exchange (NEE), in this case reported in grams of carbon per square meter (g C m⁻² yr⁻¹) over a temporal period of interest (in this case months to years). NEE is used to estimate ecosystem respiration (Reco) using an empirical model, and GPP as the difference between NEE and Reco. For comparison to WBI in trees, we report NEP as positive ecosystem uptake (i.e., negative NEE) because this sign convention matches the sign convention of WBI and GPP—carbon moving into the system is positive. NEP can be assumed to equal negative NEE by disregarding sources and sinks for CO₂ not involving conversion to or from organic carbon (Lovett et al., 2006). While some specifications of eddy covariance systems vary among sites (see Table S1 in Supporting Information S1), the differences in measurement approach and instrumentation tend to have a small overall effect on the interannual variability in eddy covariance measurements (Schmidt et al., 2012). Site-level differences in topography, homogeneity, and advection can affect the magnitude of the monthly NEP and GPP estimates. Flux records from these (and other) towers have repeatedly been synthesized to understand the drivers of ecosystem carbon cycling (Biederman et al., 2016; Curtis et al., 2002; Keenan et al., 2014). All datasets are publicly available through the AmeriFlux Network and undergo common quality control, in addition to site-specific quality control and outlier removal. We further quality-checked, filtered, and gap-filled the data as needed. We applied standardized approaches for data quality control to ensure consistent data processing across all sites and years (following those in Richardson et al. [2019]). We filtered measurements with very low horizontal wind speeds (<0.5 m s⁻¹) and removed outliers with residuals (i.e., between gap-filled and measured values) greater than six times the interquartile range (Richardson & Hollinger, 2007). Next, we used the REddyProc package (Wutzler et al., 2018) in R Statistical Software (R Core Team, 2019) for u^* (friction velocity) threshold determination, filtering, and gap filling. Gap-filled NEE data sets were then partitioned into GPP and ecosystem respiration using the nighttime partitioning technique (Reichstein et al., 2005), also in the REddyProc package.

We estimated the uncertainty of carbon uptake measurements by adjusting the u^* threshold used to exclude nocturnal periods that might underestimate nighttime respiration due to advection losses (Barr et al., 2013). The u^* threshold used to filter nocturnal data is considered one of the largest sources of uncertainty in calculating annual integrals of carbon uptake (Barr et al., 2013). We used single site-specific (i.e., fixed) u^* thresholds (see Supporting Information) to filter data with insufficient turbulence at the 5%, 50%, and 95% quantiles of the estimated u^* distributions generated using the REddyProc package. Uncertainty was then estimated as the difference between the mean u^* threshold (50% quantile) and the upper and lower quantiles. By comparing the annual variability (standard deviation) to the uncertainty, we can test whether the interannual signal exceeded the noise from measurement uncertainty.

2.2. Correlation Matrices

We used correlation matrices to identify the temporal periods of carbon uptake with the strongest correlations to WBI. This has been done previously in studies linking carbon uptake with biometric tree growth (e.g., Babst et al., 2013; Lagergren et al., 2019). Moving windows of carbon uptake integrations can be used to identify relationships that might not be apparent based on calendar-year integrals. Using this approach allows us to connect our results to our competing hypotheses (see Figure 1) and visualize the relationship between numerous periods of carbon uptake WBI simultaneously. All correlations and p values reported are based on Pearson's product moment correlation coefficient. The correlation uncertainties were calculated by taking the standard deviation of 500 Monte Carlo samples with replacement of the WBI measurements and paired integrals.

We also performed a *post hoc* analysis on the relationship between WBI and climate using the same approach as for the carbon uptake analysis. We identified how various seasonal windows of precipitation, air temperature, and incoming short-wave radiation (subsequently referred to as solar radiation) relate to WBI to determine if WBI

is also correlated to the previous year climate conditions. These variables were chosen because they are primary drivers of both WBI and carbon uptake (Zhao & Running, 2010). We used averaged gap-filled mean monthly air temperature and solar radiation collected from the eddy covariance tower, and integrated monthly precipitation from the PRISM interpolated data set (Daly et al., 2008). We also present an analysis comparing annual carbon uptake variables (NEP and GPP) with these same climate variables in the supplemental materials (Figure S2 and S3 in Supporting Information S1).

3. Data

The data and R code that support the findings of this study can be found at the repository: Teets (2022; <https://doi.org/10.5281/zenodo.6208278>). Data used to generate the daily and monthly carbon uptake data are publicly available through AmeriFlux (ameriflux.lbl.gov). The individual DOIs for each AmeriFlux site can be found in Table 1.

4. Results

4.1. Magnitude of WBI and Carbon Uptake Measurements

The mature, closed canopy forests selected for our study were net carbon sinks for all the years investigated, with average annual NEP ranging from 177 ± 30 to 346 ± 70 g C m⁻² yr⁻¹ among sites (Figure 2 and Table 2). The most productive stands (US-MMS and US-Ha1) in terms of both WBI and carbon uptake (NEP and GPP) were deciduous-dominated forests with the largest trees and highest average annual temperatures. The next most productive sites (US-Ho1, US-BAR, and US-UMB) were cold climate, northern forests that had similar mean annual temperatures but varied in species composition from conifer-dominated (US-Ho1) to deciduous-dominated (US-Bar and US-UMB). The least productive forest (US-NR1), a high-elevation conifer stand, had the lowest mean annual temperatures, least annual precipitation, and smallest tree diameters of the forests studied.

Across all sites, the average sampling uncertainty was smaller than the interannual variability for all metrics of forest productivity. The annual variability was generally lower for the two conifer-dominated forests compared to deciduous forests, but this was not always the case. The exception was WBI at US-UMB. Tree plots sampled at US-UMB displayed distinctly different trends in the late 2000s resulting from different species compositions—with one plot increasing, one plot decreasing, and one plot with relatively stable trends in WBI. The resulting average WBI had low interannual variability and high uncertainty. In contrast, the highest interannual variability in carbon uptake was found at US-Ha1, with especially high interannual variability for both NEP and GPP (Figure 2). High interannual variability of NEP at US-Ha1 was most noticeable in the years 2008–2012. It is possible that high levels of soil respiration resulting from increasing temperatures (Finzi et al., 2020) may have caused anomalously low levels of NEP in 2010–2011.

4.2. Relationship Between WBI and Carbon Uptake

We found the average annual WBI was strongly related to the average annual carbon uptake across space (average annual measurements at each site), but had weak correlations across time (based on calendar year sums of carbon uptake). In other words, sites with higher rates of carbon uptake (NEP and GPP) also had higher WBI (Figure 3), but this relationship does not predict the interannual variation in WBI. While the average carbon uptake was a good predictor of average WBI across space ($r = 0.95$ and 0.79 for NEP and GPP, respectively), individual calendar years of annual carbon uptake had much weaker associations to WBI across sites ($r = 0.28$ and 0.27 for NEP and GPP, respectively). Long-term means of carbon uptake and WBI are more strongly correlated compared to individual years likely because the averages account for potential lags in allocation (Gough et al., 2008), and because the averages will have lower sampling error compared to individual site years. On average, the magnitude of WBI accounted for the majority of the annual NEP (65%–84%), and 12%–19% of annual GPP. But in individual years, the allocation to WBI was not a simple fraction of the annual carbon uptake (Figures 3c and 3d).

Next, we tested our two competing hypotheses to determine the periods of carbon uptake (from the current and previous year) that were most strongly correlated to WBI at each site (Figure 4). The alternate hypothesis was supported at three of the six sites (US-MMS, US-Ha1, and US-Ho1), indicated by numerous significant positive correlations between WBI and carbon uptake integrals from the previous year. The null hypothesis was supported

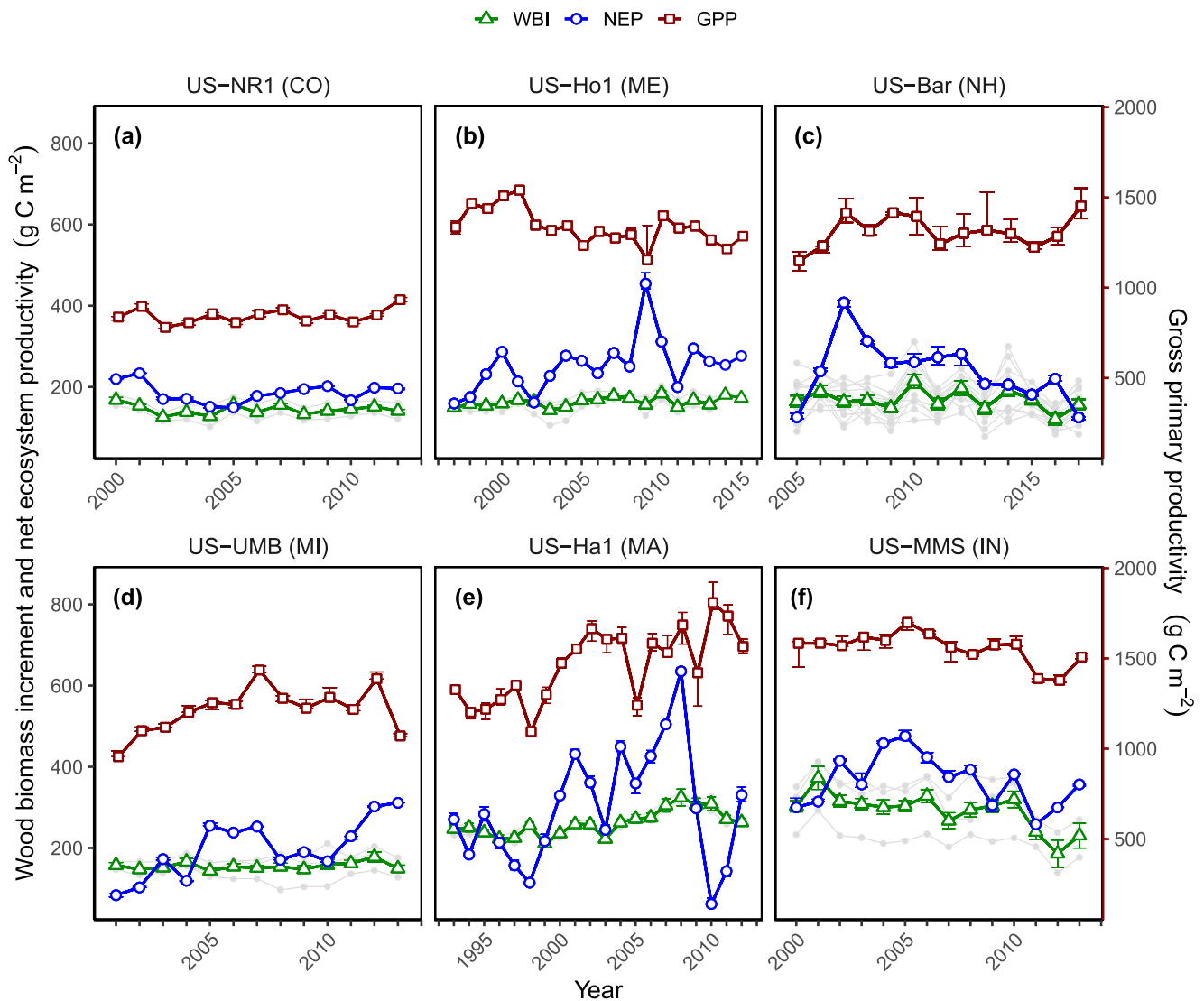


Figure 2. Annual forest productivity measurements at the six AmeriFlux sites ordered by increasing mean annual temperature. Carbon uptake measurements of NEP (blue) and GPP (red) are presented for the length of overlap with stand-level biometric tree WBI measurements (green) and plot-level WBI (gray). The scales for NEP and tree WBI are represented on the left axis and GPP on the right axis. Error bars for NEP and GPP represent the uncertainty calculated using different u^* thresholds based on 5%, 50%, and 95% quantiles estimated from 200 bootstrapped iterations. Error bars for WBI represent uncertainty based on a Monte Carlo resampling with replacement of trees. For each of 1,000 simulations, the uncertainty was calculated as the standard deviation of the difference between annual WBI and the mean of that simulation.

at one of the six sites (US-NR1), indicated by the current year's carbon uptake being a better predictor of WBI than carbon uptake from the previous year. At two of the six sites (US-UMB and US-Bar), we found relatively few significant correlations between WBI and carbon uptake, and these sites did not clearly fit either of our two competing hypotheses.

We found that WBI at the two most productive sites (US-MMS and US-Ha1) had significant positive correlations with carbon uptake over much of the current and previous years (Figure 4). This included significant positive correlations between WBI and calendar year integrals of GPP from both the current and previous years. We found that GPP was a slightly better predictor of WBI than NEP at these two sites. The temporal periods of GPP most strongly related to WBI included September of the previous year through current year April at US-Ha1 ($r = 0.69 \pm 0.10$, p value < 0.001 for GPP), and previous October through the current year September at US-MMS ($r = 0.85 \pm 0.08$, p value < 0.001 for GPP). Therefore, we find evidence for a lag in the allocation of assimilates from the previous year at these sites, but carbon uptake during the spring coinciding with growth

Table 2
Mean Annual Wood Biomass Increment (WBI), Net Ecosystem Productivity (NEP), and Gross Primary Productivity (GPP), and Ecosystem Respiration for Each Site, Listed by Increasing Mean Annual Temperature

Site, (State)	WBI $\pm \sigma_t \pm \sigma_u$ (gC/m ²)	GPP $\pm \sigma_t \pm \sigma_u$ (gC/m ²)	NEP $\pm \sigma_t \pm \sigma_u$ (gC/m ²)	Ecosystem respiration $\pm \sigma_t \pm \sigma_u$ (gC/m ²)
US-NR1, (CO)	146 \pm 15 \pm 4	838 \pm 44 \pm 12	177 \pm 30 \pm 2	US-Ha1, (MA)
US-Ho1, (ME)	161 \pm 17 \pm 6	1,331 \pm 90 \pm 14	253 \pm 64 \pm 4	US-MMS, (IN)
US-BAR, (NH)	168 \pm 34 \pm 14	1,303 \pm 86 \pm 66	245 \pm 78 \pm 2	1,058 \pm 108 \pm 68
US-UMB, (MI)	157 \pm 17 \pm 8	1,191 \pm 124 \pm 25	198 \pm 72 \pm 3	997 \pm 113 \pm 22
US-Ha1, (MA)	255 \pm 36 \pm 11	1,447 \pm 200 \pm 48	299 \pm 139 \pm 12	1,149 \pm 214 \pm 59
US-MMS, (IN)	295 \pm 47 \pm 19	1,526 \pm 91 \pm 28	346 \pm 70 \pm 4	1,180 \pm 68 \pm 29

Note. Temporal variability (σ_t) is expressed as the standard deviation of interannual variation in site-level biometric carbon increment and carbon uptake. Uncertainty (σ_u) for biometric measurements is based on Monte Carlo sampling with replacement, and for carbon uptake from different u^* thresholds listed in Supporting Information.

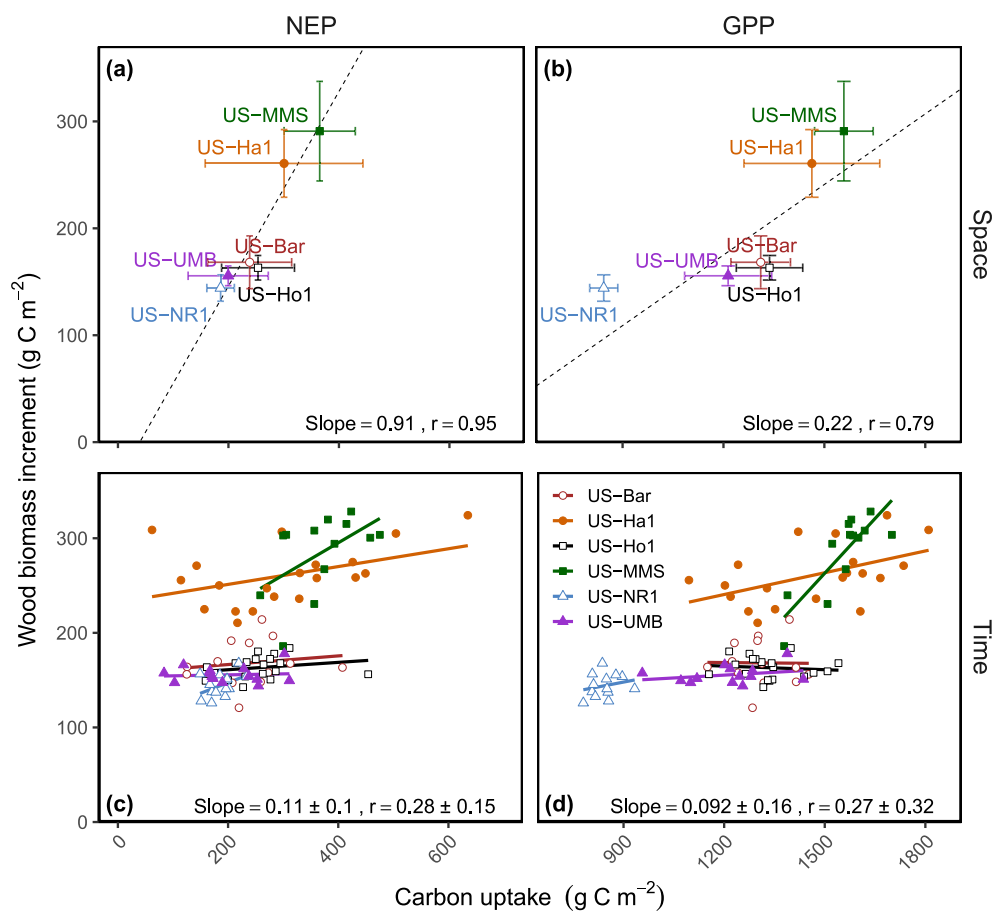


Figure 3. Wood biomass increment (WBI) compared to the annual carbon uptake (net primary productivity in panels (a) and (c) and gross primary productivity in panels (b) and (d)) for each of the six study sites. Panels (a) and (b) represent the relationship between WBI and carbon uptake across space (average annual across all site years), and panels (c) and (d) represent the relationship across time (calendar year totals). Error bars in panels (a) and (b) represent the standard deviation of the yearly totals plotted in the bottom two panels. The slopes were generated using a type II reduced major axis regression. In panels (c) and (d), the average and standard deviation of the slopes and correlations are reported across sites.

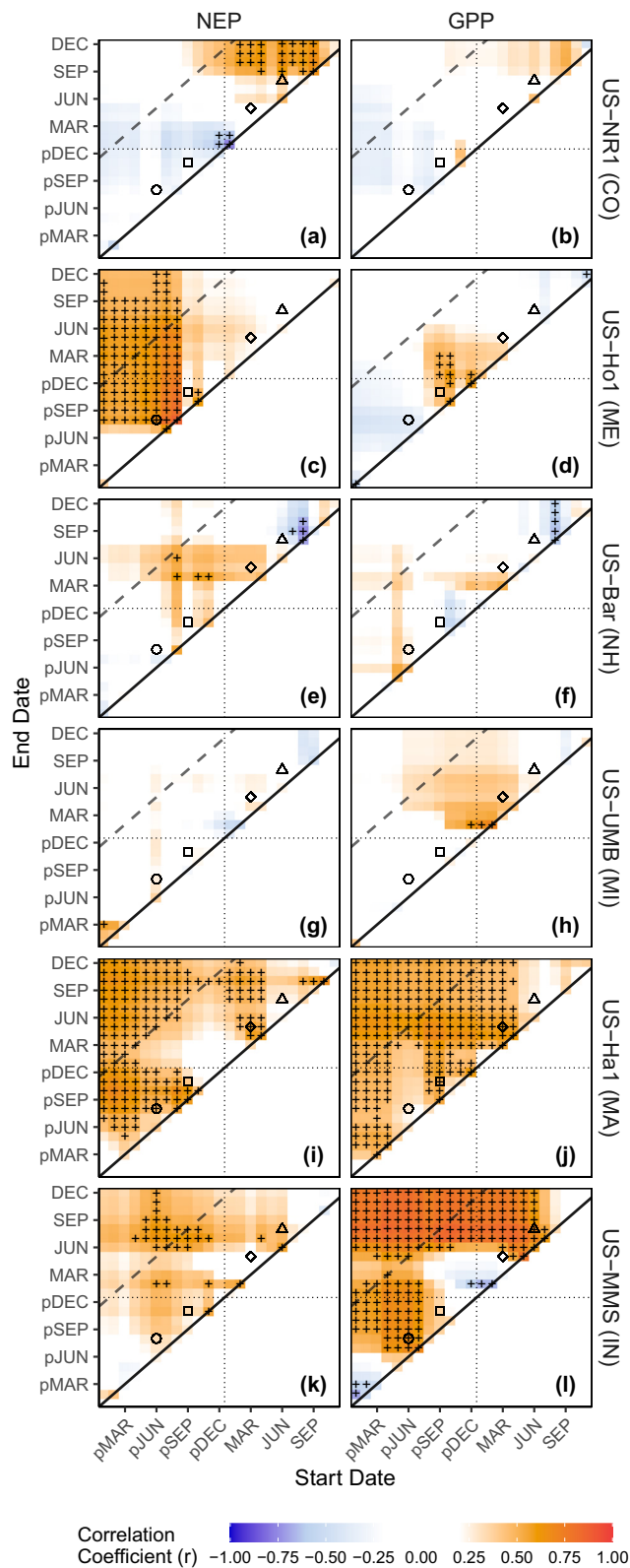


Figure 4.

was also significantly associated with growth. Carbon uptake integrals, including both previous fall and current spring, had the best agreement with WBI at these sites.

At the two conifer-dominated sites, we found very divergent relationships between WBI and carbon uptake (Figure 4). The alternate hypothesis was supported at US-Ho1 (WBI was best predicted by the previous year NEP), while the null hypothesis was supported at US-NR1 (WBI was more tightly coupled to NEP from the current year). At US-Ho1, WBI was most strongly correlated with NEP integrals that included the previous summer months. The highest correlations were found with NEP from August of the previous year—a surprisingly strong correlation for just 1 month ($r = 0.86 \pm 0.19$, p value < 0.001). In contrast, at US-NR1, WBI had significant positive correlations to NEP from current summer and fall uptake, highest from September to October ($r = 0.66 \pm 0.19$; p value = 0.01). Surprisingly, the strongest relationships at US-NR1 were negative correlations between WBI and January NEP ($r = -0.75 \pm 0.33$; p value = 0.003). Here we show two conifer-dominated forests with similar physiological traits show very different relationships between WBI and carbon uptake.

Compared to the other sites, WBI at US-UMB and US-Bar had fewer temporal periods of carbon uptake with significant correlations to WBI (Figure 4). At US-Bar, the correlations were relatively weak, with the strongest positive correlations found between WBI and NEP integrated from August of the previous year to June of the current year ($r = 0.61 \pm 0.34$; p value = 0.03). At US-UMB, the strongest correlations were found in the winter months, and were positive correlations with GPP from February ($r = 0.70 \pm 0.32$; p value = 0.007). These correlations with winter GPP were surprising because these months have negative NEP and any carbon assimilated is very small and unlikely to contribute meaningfully to WBI. We also note that WBI and US-UMB show significant relationships to winter temperatures from the same period (Figure 5), and we suspect positive correlations between temperatures and GPP in winter are resulting in the spurious relationships we see between WBI and carbon uptake in winter months (see Section 5). Overall, these sites did not clearly support the null or the alternate hypothesis.

We tested whether outliers in monthly NEP or GPP were causing spurious significant relationships with WBI that could affect the interpretation of our findings. We repeated the analysis by replacing any monthly carbon uptake values that were greater than three times the interquartile range different from the monthly median with the median values. We did not find the results and interpretations of this study were affected by extreme values of monthly carbon uptake. For more information, see Figure S1 in Supporting Information S1.

4.3. Occurrence of Lagged Allocation to Biomass Growth

The presence of lagged growth responses to carbon uptake varied widely among the sites used in this study. WBI at two sites (US-MMS and US-Ha1) demonstrated the strongest relationships to integrals including the previous year fall and current year spring. WBI at US-Ho1 was most strongly associated with previous summer carbon uptake. In contrast to all other sites, WBI at US-NR1 demonstrated significant correlations with only current year carbon uptake. We found relatively few significant relationships between WBI and carbon uptake at the two comparatively slow-growing deciduous forests (US-UMB and US-Bar). Our findings indicate that higher productivity sites (higher WBI) showed stronger relationships between WBI and carbon uptake, and those relationships oftentimes extended into the previous year. Less productive (lower WBI) sites had weaker correlations to carbon uptake, and growth was more strongly coupled to current year variables.

4.4. Relationship Between WBI and Climate Variables

Using the same correlation matrix approach as described above, we tested the relationship between WBI and precipitation, air temperature, and solar radiation from the current and previous years to detect lags in different

Figure 4. Site level correlation matrices representing the relationship between WBI and net ecosystem productivity (NEP; right panels) gross primary productivity (GPP; right panels). The sites are listed by increasing mean annual temperatures. NEP and GPP are integrated over different temporal periods (start of integral on x-axis, and end of integral on y-axis). The x- and y-axis origins represent the January of year before WBI (the prefix p refers to previous years). The dotted lines separate the two calendar years. The lower left quadrant represents only previous year integrals, the top right quadrant current year integrals, and the top left including portions of both current and previous year metrics. The dashed line represents 12 months integrals (the area above the line represents temporal periods >1 year, and the area below the line is less than 1 year). Shape outlines refer to different seasons: previous year summer (○), previous year autumn (□), spring (◇), and summer (△) uptake. Orange colors represent temporal periods with highest positive correlations with tree WBI, and cells with “+” signs represent temporal periods with significant Pearson correlation coefficients (p value < 0.05).

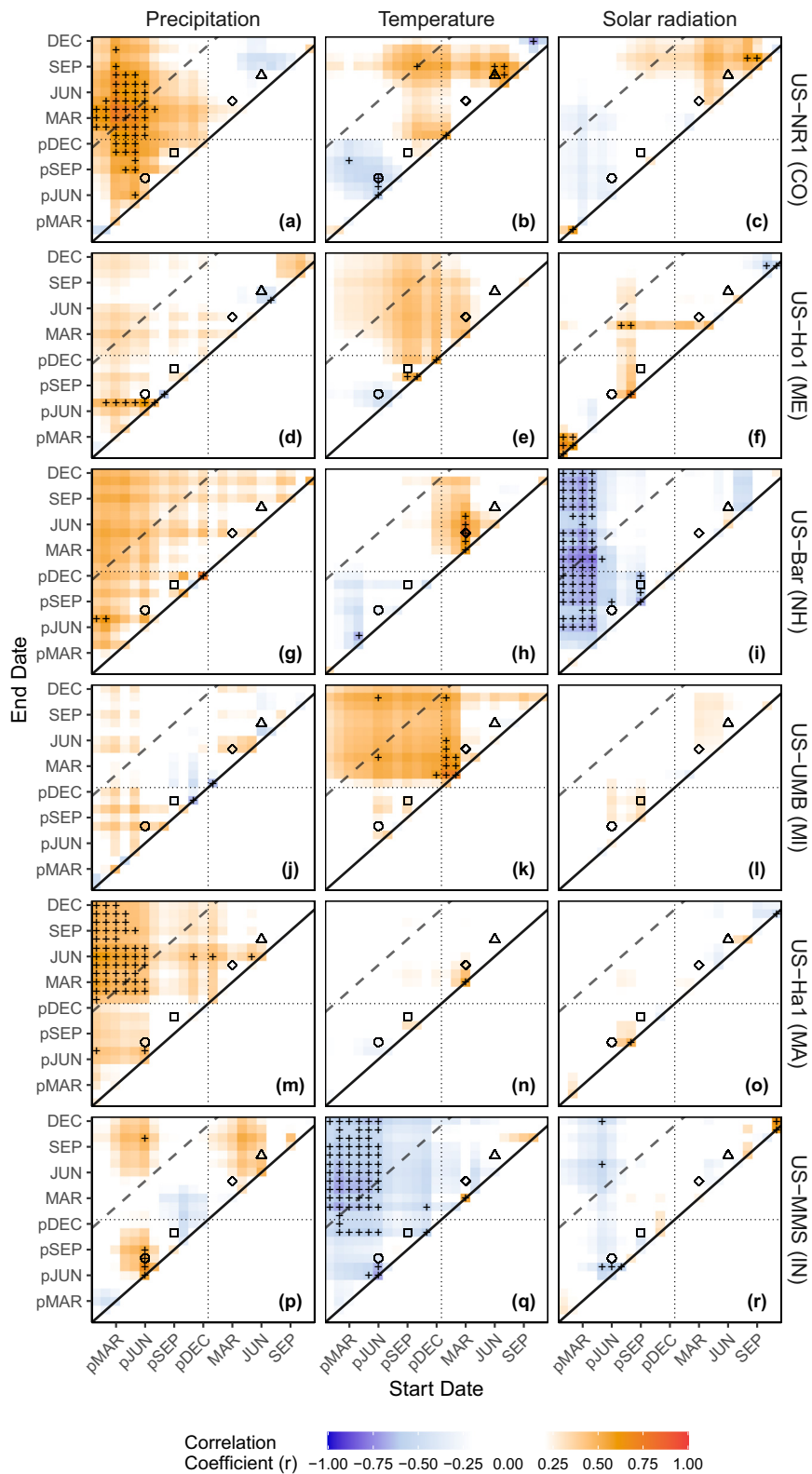


Figure 5.

climatological metrics (Figure 5). WBI at each site showed unique responses to climate variables. Sites with strong correlations between WBI and climate were sites that demonstrated relatively weak relationships between WBI and carbon uptake. For example, early season temperatures were more strongly correlated with WBI than the carbon uptake variables at US-UMB ($r = 0.74 \pm 0.32$; p value = 0.003 for February temperatures) and at US-Bar ($r = 0.78 \pm 0.34$; p value = 0.001 for March and April temperatures). Unexpectedly, solar radiation was also negatively correlated to WBI for US-Bar ($r = -0.79 \pm 0.30$; p value = 0.001 for previous April to current February), potentially due to years with higher solar radiation having lower diffuse fraction and precipitation compared to years with low solar radiation. WBI at US-NR1 was most strongly correlated with precipitation from the previous and current growing seasons ($r = 0.75 \pm 0.25$; p value = 0.003 from March of the previous year to current March). Unlike the other sites, WBI at US-NR1, US-UMB, and US-Bar were more strongly associated with climate variables than WBI was with carbon uptake.

We also found significant correlations between WBI and climate variables at the remaining sites (US-Ha1, US-MMS, and US-Ho1), but the relationships were not as strong as those between WBI and carbon uptake. WBI at US-Ha1 exhibited significant correlations to long integrals of precipitation (previous January to current June, $r = 0.60 \pm 0.13$, p value = 0.005), and spring temperature (March, $r = 0.56 \pm 0.16$, p value = 0.007). At US-MMS, WBI demonstrated significant lagged correlations to previous summer precipitation (previous June–July, $r = 0.67 \pm 0.14$, p value = 0.009), and lagged negative correlations with temperature (previous year February to current year April, $r = -0.69 \pm 0.17$, p value = 0.006). WBI at US-Ho1 demonstrated relatively weak, but significant, correlations with previous year temperature and precipitation. This analysis demonstrated that WBI in these forests is also frequently affected by lagged growth limitations from climate drivers from the previous year.

We performed a similar analysis comparing annual carbon uptake variables (NEP and GPP) to monthly climate variables in the supplemental materials (Figure S2 and S3 in Supporting Information S1). This analysis shows annual carbon uptake had differing relationships with climate variables than WBI. The climate variables with the highest positive relationships with carbon uptake tended to be from the current year (particularly for GPP), with fewer lagged relationships to climate compared to WBI. This supplemental analysis demonstrates that WBI and carbon uptake are not only affected by different environmental drivers, but the timing of the environmental drivers can differentially affect WBI and carbon uptake.

Lagged growth responses to climate variables were especially common between WBI and precipitation, with all sites demonstrating significant positive correlations between WBI and precipitation from the previous year, except for US-UMB. Current year temperature, however, was more often significantly correlated to WBI than previous year temperature.

4.5. Signal Strength in WBI

We tested our ability to detect relationships between WBI and other variables (i.e., the signal strength) at each site by taking the ratio of interannual variability (the standard deviation of annual WBI) and the uncertainty (estimated using Monte Carlo resampling of individual trees used in the analysis). We use the signal strength similar to a z-score – values greater than 2 (the interannual variability is at least twice as large as the uncertainty) suggests the interannual variability is sufficiently large to confidently detect relationships between WBI and other variables; values less than 1 suggest that the interannual variability is smaller than the uncertainty, and therefore the signal is not distinguishable from the underlying noise. We found the sites with lowest signal strength in WBI had the weakest relationships between WBI and carbon uptake (Figure 6). The two sites (US-Bar, and US-UMB) had a ratio less than two and were both cold-climate, deciduous-dominated forests that exhibited the fewest significant relationships to carbon uptake variables. The two conifer-dominated forests (US-NR1, and US-Ho1) both

Figure 5. Site level correlation matrices representing the relationship between WBI and precipitation, temperature, and solar radiation. Sites are listed by increasing mean annual temperature. Variables are integrated for precipitation and averaged for temperature and solar radiation over different temporal periods (start of integral on x-axis, and end of integral on y-axis). The x- and y-axes origins represent the January of year prior to WBI (the prefix p refers to previous years). The dotted lines separate the two calendar years. The lower left quadrant represents only previous year integrals, the top right quadrant current year integrals, and the top left including portions of both current and previous year metrics. The dashed line represents 12 months integrals (the area to above the line represents temporal periods >1 year, and the area below the line is less than 1 year). Shape outlines refer to different seasons: previous year summer (○), previous year autumn (□), spring (◇), and summer (△) uptake. Orange colors represent temporal periods with highest positive correlations with tree WBI, and cells with “+” signs represent temporal periods with significant Pearson correlation coefficients (p -value < 0.05).

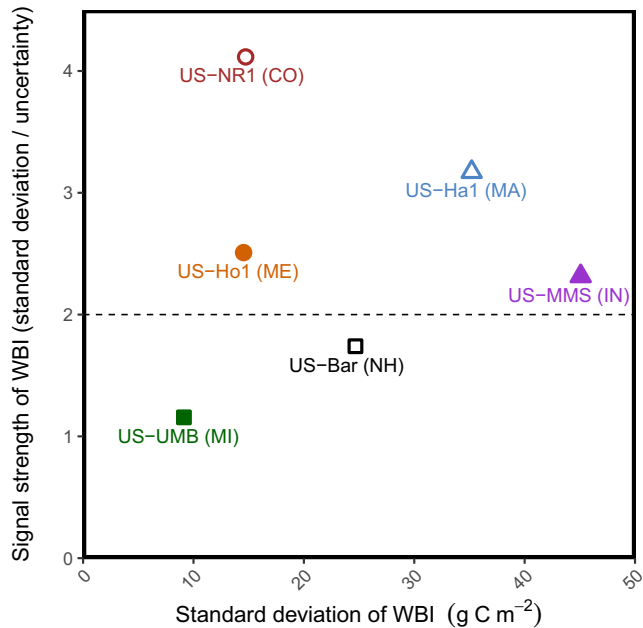


Figure 6. Signal strength of wood biomass increment (WBI) calculated as the standard deviation divided by the uncertainty plotted against the standard deviation of WBI. The horizontal dashed line at a signal strength of 2 (interannual variability was twice as strong as the sampling uncertainty), represents the threshold where relationships between WBI and carbon uptake became apparent.

expressed relatively low interannual variability, but both had relatively high signal strength due to lower tree-to-tree variability. The two most productive forests (US-Ha1 and US-MMS) had comparatively high interannual variability, and sufficient signal strength to demonstrate high correlations between WBI and carbon uptake integrals.

5. Discussion

We found strong evidence for lags in carbon allocation to tree growth at three of the six sites based on significant positive correlations between WBI and carbon uptake from the previous year. WBI at the remaining sites did not demonstrate clear relationships with previous year uptake, therefore, we did not find our alternate hypothesis (i.e., WBI is linked to previous year's carbon uptake) to be universally true across these temperate forests. Our study demonstrates that lags in the allocation of stored carbon from previous years to WBI are important mechanisms for explaining WBI, but not in all forest types. In low productivity forests, there was no clear link between WBI and previous year's carbon uptake. Weak relationships between WBI and carbon uptake in the lower productivity forests were likely due to external factors (such as environmental drivers) imposing larger limitations on growth than photosynthetic uptake. Also, the lower interannual variability at these sites makes detecting the relationships between WBI and carbon uptake more difficult, due to the higher relative uncertainty.

Our study supports previous findings that long-term averages of WBI are related to average annual NEP (Pregitzer & Euskirchen, 2004) and GPP (Waring et al., 1998; Zha et al., 2013) across space (i.e., when tested across sites). However, as expected, WBI was less tightly coupled to carbon uptake

across time when using calendar-year timescales (Figure 2). We found that WBI was consistently lower in magnitude than NEP for all sites in this study. This may be partially attributed to the growth of vegetation not included in the analysis (e.g., saplings, understory vegetation, and trees that died during the periods of interest). WBI also does not account for other sinks of carbon in reproductive tissues (Mund et al., 2010), fine root production (Gaudinski et al., 2000) and allocation to microbial symbionts (Schiestl-Aalto et al., 2019). We acknowledge the potential for systematic errors affecting long-term measurements of carbon uptake (Goulden et al., 1996; Hollinger et al., 2004) as well as from scaling up from individual-tree measurements using allometric equations (Alexander et al., 2018). Not accounting for interannual differences in tree ring density can also increase the uncertainty in the interannual variability of WBI (Babst et al., 2013; Delpierre et al., 2016). Despite these several sources of uncertainty, WBI measured in this study accounted for similar proportions of the annual NEP (Anić et al., 2018; Barford et al., 2001) and GPP (Babst et al., 2013; Litton et al., 2007; Luysaert et al., 2007; Vicca et al., 2012) reported in the literature.

The strongest relationships between WBI and carbon uptake were found at the sites with the highest WBI and highest interannual variability in WBI. Sites with low interannual variability and low signal strength in WBI had relatively weak relationships between growth and uptake. Relationships between WBI and carbon uptake may be more apparent in high-productivity forests because they are known to allocate higher proportions of recently fixed carbon to biomass growth (than to storage) compared to low-productivity forests (Litton et al., 2007; Vicca et al., 2012). Higher growth rates imply fewer environmental growth limitations, and higher demand for growing tissues. Vigorously growing trees have large, high-turnover carbohydrate pools, and growth can be fueled from a combination of current and previous year's assimilates (Carbone et al., 2013). In fertilized forests, trees can rapidly draw down storage from previous years to fuel the periods of increased growth (Goodsman et al., 2010). Here, we find that high productivity forests had growth that was more tightly coupled to carbon uptake from previous years compared to slow-growing forests.

The sites with the strongest positive correlations between WBI and carbon uptake were two deciduous dominated forests with the highest rates (and interannual variability) of WBI, highest annual temperatures, and the largest

trees of the sites studied. These sites experienced favorable conditions for wood growth over the sampling period, based on the increasing trends in carbon uptake and biomass growth in other studies (Dragoni et al., 2011; Finzi et al., 2020; Urbanski et al., 2007). WBI at these two sites (US-Ha1, US-MMS) demonstrated strong correlations to integrals of carbon uptake over much of the current and previous years, indicating WBI was fueled by a combination of stored and current year assimilates. Compared to the other sites in this study, the species compositions at US-Ha1 and US-MMS had relatively high abundances of ring-porous species (85% and 43% of the standing biomass was ring-porous species, respectively, the next highest was found at US-UMB with 25%). Ring-porous species, like those in the genera *Quercus*, initiate xylem growth before leaves develop (Tyree & Cochard, 1996; Wang et al., 1992) – starting growth earlier than diffuse-porous species (D’Orangeville et al., 2021). The large vessels in the earlywood of ring-porous species are prone to embolism in cold temperatures, and therefore the early wood formation is an adaptation to supply water to developing leaves (Zweifel et al., 2006). Therefore, these species must draw on stored nonstructural carbohydrates from previous years to initiate wood growth. An abundance of ring-porous species may be a reason for the correlations between WBI and previous year uptake at these sites.

The relative abundance of conifers versus angiosperms did not explain the differences we found in lagged relationships between WBI and carbon uptake among sites. For example, the two conifer dominated forests (US-Ho1 and US-NR1 – both dominated by *Picea* species, but with differing codominant genera) had very different relationships between WBI and carbon uptake. We expected these two conifer-dominated forests would have similar lagged relationships between WBI and carbon uptake due to their similar physiology. Compared to angiosperms (diffuse- or ring-porous species), conifers have smaller and more variable stored carbohydrate reserves (Piper & Paula, 2020). Therefore, the coupling between WBI and carbon uptake may depend on the relative amount of stored carbohydrates. An abundance of stored carbohydrates (as found in rapidly growing trees) may allow for higher correspondence between WBI and carbon uptake from the current and previous year (as seen at US-Ho1). Smaller pools of stored carbohydrates will cause growth to be more dependent on current year conditions (as seen at US-NR1). Different environmental conditions at these sites (see Hollinger et al., 1999; Monson et al., 2005) have resulted in differences in stand density (see Table 1) and stand structure. Stand density affects the amount of light penetration into the understory, and more open canopies at US-NR1 could cause carbon uptake to be more influenced by understory vegetation. Differing resource availability might also result in differences in carbon allocation to above- and below-ground resources (Friedlingstein et al., 1999). A more arid climate at US-NR1 likely requires higher carbon allocation to root growth (relative to aboveground growth) compared to eastern sites in this study (Ledo et al., 2018).

Perhaps the most prominent example of the alternate hypothesis was shown between WBI and NEP at US-Ho1. Previous work at US-Ho1 had also found WBI responds to previous year’s NEP (Richardson et al., 2013; Teets et al., 2018) and these studies were a major motivation for the development of the alternate hypothesis. Our findings here further support the importance of previous year’s carbon uptake (and climate variables) for WBI at US-Ho1. We predicted uptake occurring late in the growing season would be strongly associated with WBI in the following year because wood formation in northern forests largely occurs in the spring and early summer (D’Orangeville et al., 2021; Rossi et al., 2006) and ends well before carbon uptake slows down in the winter (Zweifel et al., 2010). Our findings here suggest that uptake from the previous year’s summer months was strongly linked to WBI the following year in this evergreen-dominated northern forest, but this does not necessarily translate to other temperate (or conifer-dominated) forests.

The relationships between WBI and carbon uptake at US-Bar were less apparent than other northeastern sites in this study. Similarly, Ouimette et al. (2018) also found that WBI was weakly correlated to current and previous calendar year integrals of uptake at the same site. Our results show WBI exhibited few significant lagged relationships to carbon uptake from the previous summer through current spring, but these relationships were not strong enough to support our alternate hypothesis. WBI was more tightly coupled to current year climate conditions (notably spring temperature). One of the dominant species at US-Bar (*Fagus grandifolia*) is persistently affected by beech bark disease (Leak & Smith, 1996) and has prolific understory resprouting (Pontius et al., 2016). As a result, stand-level growth is negatively affected by relatively high levels of disturbance from pests and tree-to-tree competition compared to other sites. Higher levels of disturbance, and low signal strength in WBI compared to other northeastern sites may cause relatively weak correlations between WBI and carbon uptake at US-Bar.

The site with the lowest signal strength in WBI (US-UMB) did not show significant correlations to any temporal periods with positive NEP, unlike all other sites. This forest showed comparatively little interannual variability in WBI, also noted by Gough et al. (2010), despite changes in the dominant tree species—where early successional species are being replaced by middle-successional and late-successional tree species. We suspect the relatively low interannual variability and high uncertainty in WBI affected our ability to find a clear relationship with carbon uptake. Alternatively, a lack of relationships between WBI and carbon uptake might suggest WBI is limited by factors other than carbon supply (Fatichi et al., 2014). In forests experiencing higher levels of growth limitation, the amount of carbon assimilated can exceed what is needed for growth (Körner, 2003). Despite the low signal strength, WBI at US-UMB was significantly correlated to GPP in January and February, months with very low rates of carbon uptake that can only contribute a minimal quantity of assimilates to WBI. It is likely these significant correlations are due to correlation between winter temperatures and winter GPP. Warm late-winter temperatures in northern forests can hasten snow melt and can lead to earlier (and increased) tree growth (Tardif et al., 2001) and carbon uptake (Keenan et al., 2014; Richardson et al., 2010). Therefore, we infer that the relationships between WBI and late winter GPP at US-UMB are spurious relationships with very little biological justification.

The only high elevation site used in this study (US-NR1) was also the only site to support the null hypothesis—that WBI exhibits strong positive correlations to current year, and not previous year, carbon uptake. We found WBI at US-NR1 had significant positive correlations to NEP from the summer and fall corresponding to growth, and showed very little reliance on previous year uptake. WBI was also positively correlated to summer temperatures over the same periods. Warm conditions in the days and nights of summer months are favorable for wood formation in high elevation forests (Körner, 1998). Interestingly, WBI also demonstrated significant negative correlations to winter NEP. This may be explained by the counteracting effects of warm winter temperatures and snow depth in forests that receive most of their precipitation as winter snowfall. Warm conditions at US-NR1 may have positive effects on NEP in the late winter and spring months, but also result in decreased water availability in the summer (Hu et al., 2010; Monson et al., 2005). With sufficient precipitation and warm summer temperatures, we see increases in WBI (this study) and photosynthetic uptake (Monson et al., 2005). Despite significant positive relationships with current year carbon uptake, WBI at US-NR1 was more tightly coupled to recent environmental drivers than to metrics of carbon uptake, and showed no evidence of being limited by carbohydrates carried over from previous years. This is supported by findings that growth is unlikely to be limited by carbon supply in cold-climate, high elevation forests (Hoch & Körner, 2012).

6. Conclusions

We find the link between WBI and previous year's carbon uptake not only varies among sites, but it largely depends on the rates of wood biomass growth (Friedlingstein et al., 1999) and the external controls on growth. Based on our results, species composition (i.e., the relative abundance of conifers) was not the primary driver of differences found between sites—indicated by the two conifer-dominated forests having very different relationships between WBI and carbon uptake. Instead, the link between WBI and carbon uptake was better explained by forest productivity. Compared to low productivity forests, we found WBI in more productive forests had higher interannual variability (thus higher signal-to-noise ratios), and higher correlations to carbon uptake—with correlations often extending into the previous year. Vigorously growing forests allocate higher proportions of carbon uptake to aboveground biomass compared to slow-growing forests (Hilbert & Reynolds, 1991; Litton et al., 2007; McMurtrie & Dewar, 2013) making the correlation between WBI and carbon uptake more apparent. Stressful environmental conditions can cause the increased allocation to storage as nonstructural carbohydrates (Hoch & Körner, 2012), or fine roots (Kobe et al., 2010) at the expense of structural growth. When structural growth is limited by factors other than photosynthesis (e.g., Lempereur et al., 2015; Mund et al., 2010), WBI can become decoupled from photosynthetic uptake (Muller et al., 2011; Pompa-García et al., 2021).

In summary, our results show evidence that the previous year's carbon uptake is an important driver in explaining annual WBI in some temperate forests. Inconsistent relationships between WBI and carbon uptake in previous studies may have been partially due to lags in allocation of carbon to growth, but other factors such as forest productivity and climate, likely also play important roles. Our findings suggest forest productivity is an important determinant of the use of previously assimilated carbon uptake for tree growth. Forests with strong growth sinks

in WBI can use a combination of carbohydrates from the current year and previously stored assimilates, whereas weak growth sinks are more likely to be limited by current year conditions.

Data Availability Statement

The authors acknowledge the following AmeriFlux sites for their data records: US-NR1, US-Ho1, US-Bar, US-UMB, US-Ha1, and US-MMS. The data and R code that support the findings of this study can be found at the repository: Teets (2022; <https://doi.org/10.5281/zenodo.6208278>). Data used to generate the daily and monthly carbon uptake data are publicly available through AmeriFlux (ameriflux.lbl.gov). The individual DOIs for each AmeriFlux site can be found in Table 1.

Acknowledgments

Funding for AmeriFlux data resources and these core flux sites was provided by the U.S. Department of Energy's Office of Science. AFT would like to thank Anthony J. Garnello for thoughtful feedback to the early stages of the manuscript. The authors acknowledge support from the National Science Foundation (awards DEB 1637685, 1741585, and 1832210). SF acknowledges support from Maine Agricultural and Forest Experiment Station (#ME042118). Research at the Bartlett Experimental Forest is supported by the USDA Forest Service's Northern Research Station. NCAR is sponsored by the National Science Foundation.

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