Received: 13 September 2019 | Revised: 6 December 2019 | Accepted: 10 December 2019

DOI: 10.1111/gcb.14971

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Biomass increases attributed to both faster tree growth and altered allometric relationships under long-term carbon dioxide enrichment at a temperate forest

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Funding information

US Department of Energy; National Institute for Global Environmental Change; US Forest Service Southern Research Station

Abstract

Increases in atmospheric carbon dioxide (CO_2) concentrations are expected to lead to increases in the rate of tree biomass accumulation, at least temporarily. On the one hand, trees may simply grow faster under higher CO_2 concentrations, preserving the allometric relations that prevailed under lower CO_2 concentrations. Alternatively, the allometric relations themselves may change. In this study, the effects of elevated CO_2 (eCO_2) on tree biomass and allometric relations were jointly assessed. Over 100 trees, grown at Duke Forest, NC, USA, were harvested from eight plots. Half of the plots had been subjected to CO_2 enrichment from 1996 to 2010. Several subplots had also been subjected to nitrogen fertilization from 2005 to 2010. Allometric equations were developed to predict tree height, stem volume, and aboveground biomass components for loblolly pine (*Pinus taeda* L.), the dominant tree species, and broadleaved species. Using the same diameter-based allometric equations for biomass, it was estimated that plots with eCO_2 contained 21% more aboveground biomass, consistent with previous studies. However, eCO_2 significantly affected allometry, and these changes had an additional effect on biomass. In particular, *P. taeda* trees at a given diameter were observed to be taller under eCO_2 than under ambient CO_2 due to changes in both the allometric scaling exponent and intercept. Accounting for allometric change increased the treatment effect of eCO_2 on aboveground biomass from a 21% to a 27% increase. No allometric changes for the nondominant broadleaved species were identified, nor were allometric changes associated with nitrogen fertilization. For *P. taeda*, it is concluded that eCO_2 affects allometries, and that knowledge of allometry changes is necessary to accurately compute biomass under eCO_2. Further observations are needed to determine whether this assessment holds for other taxa.

KEYWORDS

biomass, carbon dioxide, carbon storage, climate change, elevated CO_2, free-air CO_2 enrichment, loblolly pine, tree allometry, tree height, wood density

1 | INTRODUCTION

Carbon storage in terrestrial living plant biomass (380–536 Pg C; Erb et al., 2018) is expected to increase as atmospheric carbon dioxide (CO_2) concentrations increase (Ciais et al., 2013; Gregory, Jones, Cadule, & Friedlingstein, 2009). Free-air CO_2 enrichment (FACE) experiments have assessed individual plant- and ecosystem-scale responses of forests to elevated CO_2 (eCO_2), and have found that trees subjected to eCO_2 typically showed greater photosynthesis (Bader, Siegwolf, & Korner, 2010; Ellsworth et al., 2012; Schäfer et al., 2003), and those stands have attained higher net primary productivity (NPP; Gonzalez-Benecke, Teskey, Dinon-Aldridge, & Martin, 2017; McCarthy et al., 2010; Norby et al., 2005) and biomass (McCarthy et al., 2010; Talhelm et al., 2014).

Estimation of tree biomass, as has been done in analysis of the forest FACE experiments, generally requires the use of allometric relationships. These relationships are contingent on biometric measurements of tree size (typically diameter at breast height [DBH]) and an allometric equation that estimates plant biomass from the biometric measurements. If an eCO_2 treatment results in a larger stand biomass than ambient CO_2 (aCO_2), eCO_2 must have either caused trees to move more rapidly along fixed allometric curves, shifted the allometric curves themselves, or both.

While previous analyses of FACE experiments showed that eCO_2 can increase both tree diameter and height relative to aCO_2 (DeLucia et al., 1999; Liberloo et al., 2009; McCarthy et al., 2010; Norby, Warren, Iversen, Medlyn, & McMurtrie, 2010), the effects of eCO_2 on allometry have been more difficult to ascertain, perhaps due to insufficiently long time series. Using 5 years of data, no statistically significant effects of eCO_2 on the relationship between DBH and tree height (H) of *Pinus taeda* at Duke Forest FACE were found (DeLucia, George, & Hamilton, 2002; McCarthy et al., 2010). Similarly, FACE studies of 1–6 years' duration did not find a significant effect of eCO_2 on allometric equations linking DBH to either stem biomass or to aboveground woody (stem + branch) biomass (Calfapietra et al., 2003; King et al., 2005; Liberloo et al., 2006; Norby, Todd, Fults, & Johnson, 2001). Consequently, most previous FACE biomass analyses have assumed no effect of eCO_2 on these allometric equations (Calfapietra et al., 2003; DeLucia et al., 1999; King et al., 2005; Liberloo et al., 2006; Norby et al., 2001, 2005; Schäfer et al., 2003; Talhelm et al., 2014). Intriguingly, a study analyzing one of the longest time series (8 years) suggested that an eCO_2 effect on the DBH-stem biomass allometric equation may be emerging: without accounting for eCO_2, this equation was shown to have increasing bias as a function of time or ontogeny (McCarthy et al., 2010).

Despite the importance of foliage and branch biomass with respect to tree- and canopy-level physiological functioning (Bentley et al., 2013; Enquist et al., 2007), the effects of eCO_2 on allometric equations for foliage and branches have rarely been reported. For example, increases in the branch-to-stem biomass ratio of *Populus* species in eCO_2 (Liberloo et al., 2006) may indicate an eCO_2 effect on the allometric equation for branch biomass, although this possibility was not explicitly evaluated. Meanwhile, Talhelm et al. (2014) developed allometric equations for branch and foliage biomass at Aspen FACE, but the effects of eCO_2 on the equation were not provided.

Finally, the literature is marked by disagreement on the effects of eCO_2 on wood density, which must either implicitly or explicitly enter into allometric equations linking size to biomass (Ceulemans, Jach, Velde, Lin, & Stevens, 2002; Kilpelainen, Peltola, Ryyppo, & Kellomaki, 2005; McCarthy et al., 2006; Oren et al., 2001; Telewski, Swanson, Strain, & Burns, 1999). Studies investigating effects on wood density have mainly analyzed short-term treatments. Telewski et al. (1999) found a significant increase in total wood density of *P. taeda* seedlings in eCO_2 under nonlimiting nutrient conditions due to an increase in latewood maximum density. Domec, Schäfer, Oren, Kim, and McCarthy (2010) also found positive effects of eCO_2 on cell wall thickness of *P. taeda* branches. Oren et al. (2001) observed a decrease of wood density of *P. taeda* after the first 3 years of CO_2 enrichment at Duke FACE site. The densities in earlywood and latewood of *Pinus sylvestris* were slightly reduced (1%–6%) with 3–6 years of eCO_2, but the changes were not statistically significant (Ceulemans et al., 2002; Kilpelainen et al., 2005).

The apparent absence of an eCO_2 effect on tree allometry is surprising because tree geometry, and in particular the relationship between diameter and height, has been shown to be affected by other environmental factors (Chave et al., 2014; Duncanson, Dubayah, & Enquist, 2015; Hulshof, Swenson, & Weiser, 2015; Ibáñez, Zak, Burton, & Pregirzer, 2016; Lines, Zavala, Purves, & Coomes, 2012; Samuelson et al., 2014; Voelker et al., 2017; Way & Oren, 2010). For example, the DBH–H relationship may be modulated by plant–water relations. At a given DBH, H may create hydraulic constraints on water transport and productivity (Falster & Westoby, 2003; Ryan & Yoder, 1997; Schäfer, Oren, & Tenhunen, 2000). eCO_2 may alter hydraulic allometry index (sapwood area divided by the product of leaf area and H) and xylem hydraulic conductivity (Domec, Smith, & McCulloh, 2017; Ward et al., 2013). Both decreases in hydraulic allometry index (Ward et al., 2013) and unaltered leaf-to-sapwood ratio in eCO_2 (McCarthy et al., 2007; Pataki, Oren, & Tissue, 1998) may indicate a greater H at a given DBH in eCO_2. Furthermore, increased overstory leaf area and thus canopy radiation interception in eCO_2 (Kim, Oren, & Qian, 2016; McCarthy et al., 2007) may provide conditions favoring H growth over DBH growth, especially for trees receiving low light in the subcanopy.

An effect of eCO_2 on allometry would also be expected if eCO_2 accelerates stand development. Allometry is known to be sensitive to stand age, with trees in older stands being taller for their diameter than trees in younger stands (Lappi, 1997; McCarthy et al., 2010; Sumida, Miyaura, & Torii, 2013). It has also been suggested that stands in eCO_2 would have accelerated development (Hasegawa et al., 2018; Körner, 2006; Pretzsch, Biber, Schütze, Uhl, & Rötzer, 2014). For example, Pretzsch et al. (2014) found that increased CO_2 concentrations and N deposition, along with extended growing seasons and higher temperature, contributed to faster stand volume growth of *Picea abies* and *Fagus sylvatica* in 1961–2010 than the growth in 1870–1960. Thus, at least on a qualitative level, stand age and eCO_2 should have similar effects on allometry.

Here, we evaluated whether 15 years of CO_2 enrichment, six of which with nitrogen (N) amendment, at the Duke FACE site changed the allometric relationships and aboveground biomass of the mid-canopy to dominant *P. taeda*, and mixed broad-leaved species positioned from the understory to the canopy. Our time series is approximately double the length of time series that have previously been used to evaluate allometry under eCO_2. Specifically, we explored the effects of CO_2 enrichment with and without N fertilization on (a) DBH–*H* relationships; (b) tree-level allometric equations for biomass; and (c) stand-level aboveground biomass accumulation. If eCO_2 accelerates tree growth and stand development, DBH–*H* relationship in eCO_2 may be similar to that of an older stand. Thus, we first hypothesize that eCO_2 allows greater *H* at a given DBH (H1). We allowed for the possibility of changes to both the allometric scaling exponent and the intercept. Second, we evaluated the effects of eCO_2 on a DBH-stem volume allometric equation, on the vertical variations of wood and bark densities, and on allometric equations for branch and foliage biomass, and hypothesized that the DBH-biomass allometric relationship derived from aCO_2 conditions will underpredict biomass in eCO_2 because it does not account for increased height under eCO_2 (H2). Finally, because N fertilization often increased growth and biomass of *P. taeda* (Borders et al., 2004; King, Seiler, Fox, & Johnsen, 2008; Menge, Grand, & Haines, 1977), and because enhanced tree growth in eCO_2 may deplete soil N over time and reduce the enhanced plant biomass production (Finzi et al., 2006; Luo et al., 2004; Oren et al., 2001), we hypothesized that N amendment would support the enhanced productivity of trees in eCO_2, resulting in greater biomass in N-fertilized plots than that in unfertilized plots (H3).

2 | MATERIALS AND METHODS

2.1 | Site description

This study was based on measurements from the Duke Forest FACE site in North Carolina, USA (36°58′N, 79°06′W). *P. taeda* seedlings (3-year-old) were planted after clear-cutting and burning in 1983. Naturally regenerated broad-leaved species, including *Liquidambar styraciflua*, *Ulmus alata*, *Acer rubrum*, and *Fraxinus americana*, were common in the understory, and accounted for ~41% of total leaf area of the site during growing season in 2009 (Kim et al., 2017).

The site included eight 30-m-diameter circular plots. The FACE experiment started with two plots in 1994: one reference plot and one prototype plot under CO_2 enrichment, targeted at 200 μmol/mol above the ambient atmospheric CO_2 concentration. The experiment expanded with six additional plots (three eCO_2 and three aCO_2 plots) on 27 August 1996. Because the CO_2 enrichment in 1996 began near the end of the growing season, measurements in 1996 were considered to be pretreatment. Average DBH and tree height of *P. taeda* in 1996 were 15.2 cm and 11.8 m, respectively; they were not different by the CO_2 enrichment (DeLucia et al., 1999; McCarthy et al., 2010). From 1998–2004, a nutrient addition experiment was added to the two original plots. A complete fertilization was applied annually to half of each plot depending on the nutrient requirements for that year (Albaugh, Allen, Dougherty, Kress, & King, 1998; Linder, 1995). The nutrient addition experiment expanded to other six plots in 2005 with a common protocol of N-only fertilization (ammonium nitrate pellets; NH_4NO_3; 11.2 g N m^{-2} $year^{-1}$). Each half-plot was separated with an impermeable barrier inserted 70 cm into the soil, which is the depth of the fine root system at the site (Matamala & Schlesinger, 2000). The CO_2 enrichment concluded on 31 October 2010. All aboveground biomass in ~40% of each plot, half under native soil conditions and half receiving N fertilizer, was harvested between late 2010 and early 2011.

2.2 | Data collection

In each plot, DBH was measured annually from 1996 to 2010 for all trees with DBH >2 cm by survey or spring-loaded dendrometer bands (Moore et al., 2006). The dendrometer bands were installed on trees with DBH >8 cm. *H* and height-to-crown base (HCB; distance from the ground to the bottom of the live crown) were measured with either a height pole or a survey laser (Criterion 400; Laser Technology Inc.). *H* was measured for a subset of trees in 1996, 1997, 2000, 2001, and 2004, and for all trees in 2005–2010. HCB measurements were measured annually from 2005 to 2010.

Diameter at breast height, *H*, HCB, and vertical crown length (CL; distance from the top to the bottom of the live crown) were measured for all individuals that were harvested in 2010–2011. From each plot, 10 *P. taeda* (including both dominant and suppressed trees) and large (DBH > 8 cm) broad-leaved species were selected for additional analyses: development of allometric equations for plant volume and biomass, estimation of densities of stem wood and stem bark. For these trees, all branches with foliage were collected. Approximately 10% of these branches were cut at the beginning of the harvest to calculate specific leaf area (SLA) before leaf senescence started. SLA was calculated with dry weight and projected leaf area, which was measured using ImageJ software (NIH; https://imagej.nih.gov/ij/). For *P. taeda*, branch heights and diameters at the branch base were measured. Also, for *P. taeda*, stem disk samples were collected at tree base, at breast height (~1.3 m) and at the top of every 4-m section above breast height. For broad-leaved species, three stem disk samples per tree were collected at breast height, at the mid-point of the entire stem and at two-thirds the distance from the bottom of the crown.

Measurements on each stem disk sample included diameter, inside-bark diameter, thickness of disk, and tree ring widths. Four diameter measurements spaced 45° from each other were taken and the root mean square of the four measurements was used as the diameter of a stem disk. Stem disk samples were oven-dried at 65°C for 1 week and weighed. Each tree crown was vertically divided into three parts (top, middle, and bottom crowns), and one representative branch and five representative foliage excisions (five fascicles per cohort for *P. taeda*) from each crown part were subsampled to calculated wood density and SLA. A 10 cm section of each branch subsample was suspended in water to measure the volume of the section. The density of branch wood was calculated by dividing the volume of the branch section from its dry weight. All live branches and foliage of each tree were oven-dried at 65°C for 1 week and weighed to estimate the biomass of branch and foliage.

2.3 | Allometric relationships

We adopted a traditional formulation in which we computed year-specific and treatment-specific stand-level relationships between DBH and *H* for either *P. taeda* or combined broad-leaved species:

$$H_t = \beta_{t1} + \beta_{t2} D_t + \varepsilon_t, \tag{1}$$

where H_t is the logarithm of *H* in year *t* (m) and D_t is the logarithm of DBH in year *t* (cm), β_{t1} and β_{t2} are regression coefficients, and ε_t is an error term. We then evaluated the treatment effects of eCO_2 and N fertilization on year-specific DBH–*H* allometry according to:

$$\begin{aligned} H_t = {} & \beta_{t1} + \beta_{t2} D_t + \beta_{t3} C + \beta_{t4} \left(D_t \times C\right) + \beta_{t5} N + \beta_{t6} \left(D_t \times N\right) \\ & + \beta_{t7} \left(C \times N\right) + \varepsilon_t, \end{aligned} \tag{2}$$

where H_t is the logarithm of *H* in year *t* (m) and D_t is the logarithm of DBH in year *t* (cm), *C* is the CO_2 treatment (0 for aCO_2 and 1 for eCO_2 treatments), *N* is the N treatment (0 for unfertilized and 1 for N-fertilized treatments), the β_t are regression coefficients, and ε_t is an error term.

To measure stem volume of harvest trees, we first excluded ~21% of selected trees with abnormal structure, such as a split stem or a broken top, or missing data, leaving a total of 59 trees for *P. taeda* and 50 trees for broad-leaved species across all treatments. The stem wood volumes of these trees were calculated with the overlapping-bolts method (Bailey, 1995) using inside-bark diameter of stem disk samples. The volume of the top section was obtained using a formula for conoid section and the volume of the overlapped section was obtained using Newton's formula:

$$v_i = \begin{cases} \frac{\pi}{12} d^2_{i,\mathrm{bot}} L_i, & i = 1 \\ V_{i-1} - v_{i-1}, & i = 2, 3, \cdots, n, \text{where } n \text{ is the butt section}, \end{cases} \tag{3}$$

$$V_i = \frac{\pi}{24} \left(D^2_{i,\mathrm{bot}} + 4D^2_{i,\mathrm{mid}} + D^2_{i,\mathrm{top}} \right) \left(L_i + L_{i+1} \right), \tag{4}$$

where v_i is the volume of a section *i*, $d_{\mathrm{i,bot}}$ is the diameter at the bottom of a section, L_i is the length of a section, V_i is the combined volume of two sections (*i* and *i* + 1), $D_{i,\mathrm{bot}}$, $D_{i,\mathrm{mid}}$, $D_{i,\mathrm{top}}$ are the diameters at the bottom, middle, and top of the combined section, respectively. Stem bark volume of each tree was obtained by calculating stem total volume with the overlapping-bolts method using outside-bark diameter and subtracting stem wood volume from it.

Volumes of stem wood, stem bark, and stem total were estimated with CO_2 and N treatments as fixed effects, and with either DBH only (Equation 5) or with both DBH and *H* (Equation 6) as additional predictors:

$$V_{\mathrm{stem}} = \beta_{s1} + \beta_{s2} D + \beta_{s3} C + \beta_{s4} \left(D \times C\right) + \beta_{s5} N + \beta_{s6} \left(D \times N\right) + \beta_{s7} \left(C \times N\right) + \varepsilon_{s1}, \tag{5}$$

$$\begin{aligned} V_{\mathrm{stem}} = {} & \beta_{s8} + \beta_{s9} D + \beta_{s10} C + \beta_{s11} \left(D \times C\right) + \beta_{s12} N + \beta_{s13} \left(D \times N\right) + \beta_{s14} \left(C \times N\right) \\ & + \beta_{s15} H + \beta_{s16} \left(D \times H\right) + \beta_{s17} \left(H \times C\right) + \beta_{s18} \left(H \times N\right) + \varepsilon_{s2}. \end{aligned} \tag{6}$$

where V_{stem} is the logarithm of stem volume (m^3), *D* is the logarithm of DBH (cm), *H* is the logarithm of *H* (m), *C* is the CO_2 treatment (0 for ambient and 1 for eCO_2), *N* is the N treatment (0 for unfertilized and 1 for N-fertilized), β_s are regression coefficients, and ε_s are error terms.

The stem wood and stem bark densities of each stem disk sample were calculated with dry weight and fresh volume. Based on the relationships between the wood and bark density of stem disks and the locations of the stem disk samples (i.e., the distances of the stem disk from tree top), stem wood and stem bark densities at 1.3 m were identified with tree-level average density (Antony, Schimleck, & Daniels, 2012).

The effects of CO_2 and N on allometric equations for the biomass of *P. taeda* branches, *P. taeda* foliage, and combined broad-leaved species branches were tested with DBH as a covariate:

$$B = \beta_{b1} + \beta_{b2} D + \beta_{b3} C + \beta_{b4} N + \beta_{b5} \left(C \times N\right) + \varepsilon_{b1}, \tag{7}$$

where *B* is the logarithm of branch or foliage biomass (g), β_b are regression coefficients, and ε_b is an error term. We also investigated a more complex formulation in which CL and basal area percentile (BAP) were considered as additional variables. The BAP is the percentile ranking of a tree when compared with the basal area of all trees within the stand (Stage, 1973). The BAP was calculated as:

$$\mathrm{BAP}_{ij} = \left\{ 1 - \frac{\mathrm{BAL}_{ij}}{\mathrm{BA}_i} \right\} \times 100, \tag{8}$$

where BAP_j is the BAP of a tree *j* within a stand *i*, BAL_{ij} is the sum of the basal area of all trees larger than tree *j*, BA_i is the sum of the basal area of all trees in the stand *i*. Because broad-leaved species at this site was located mainly in the subcanopy, an ability to maintain a higher rate of photosynthesis at low light condition (i.e., shade tolerance or ST) is one of the key characteristics of trees to survive and grow (Burns & Honkala, 1990). Thus, for combined broad-leaved species, the species-level ST, which was classified as shade-tolerant or shade-intolerant based on Burns and Honkala (1990), Farrar (1995) and Harlow, Harrar, Hardin, and White (1996), was also accounted for:

$$\begin{aligned} B = {} & \beta_{b6} + \beta_{b7} D + \beta_{b8} \mathrm{CL} + \beta_{b9} \mathrm{BAP} + \beta_{b10} \mathrm{ST} + \beta_{b11} C \\ & + \beta_{b12} N + \beta_{b13} (C \times N) + \varepsilon_{b2}, \end{aligned} \tag{9}$$

where *B* is the logarithm of branch biomass (g). Foliage data of broad-leaved species were not used to develop allometric equations due to senescence concurrent with the harvest period. Instead, allometric equations for foliage biomass of the same or similar species in Clark, Phillips, and Frederick (1986) were used to estimate foliage biomass of broad-leaved species in the stand.

2.4 | Biomass estimation

Aboveground biomass of *P. taeda*, combined broad-leaved species, and the total stand during the experimental period (1996–2010) were calculated using the allometric equations and biometric measurements. Missing DBH measurements (3.7% of measurements) were gap filled by linear interpolation. Missing *H* of *P. taeda* (52%–100% in 1996–2004; 1%–3% in 2005–2010) and combined broad-leaved species (91%–100% in 2001–2005; 18%–29% in 2006–2010) were gap filled using regression models with DBH, BAP, tree age, and CO_2 treatment:

$$\begin{aligned} H = {} & \beta_{h1} + \beta_{h2} D + \beta_{h3} \mathrm{BAP} + \beta_{h4} \mathrm{AGE} + \beta_{h5} C + \beta_{h6} \left(D \times \mathrm{BAP} \right) + \beta_{h7} \left(D \times \mathrm{AGE} \right) \\ & + \beta_{h8} \left(D \times C \right) + \beta_{h9} \left(\mathrm{BAP} \times \mathrm{AGE} \right) + \beta_{h10} \left(\mathrm{BAP} \times C \right) + \beta_{h11} \left(\mathrm{AGE} \times C \right) + \varepsilon_h, \end{aligned} \tag{10}$$

where BAP and AGE are the logarithm of BAP and tree age. The *H* of broad-leaved species from 1996 to 2000 was not estimated because the *H* of broad-leaved species was not measured before 2001.

The stem biomass of *P. taeda* of this study was compared to previous estimates available up to 2004 at the same site (McCarthy et al., 2010). To compare the two estimates for the entire experimental period, stem biomass of *P. taeda* in 1996–2010 were re-calculated based on the following methods used in the previous study: (a) gap filling of missing *H* using plot- and year-specific DBH–*H* relationships for years with *H* measurements and using relative DBH increments for years without *H* measurements; (b) an allometric equation for stem volume from Fang, Borders, and Bailey (2000); (c) constant stem wood and stem bark densities from Naidu, DeLucia, and Thomas (1998).

2.5 | Statistical analysis

The effects of CO_2 enrichment and N fertilization on biometric variables, allometric relationships and biomass were evaluated through linear mixed effect models (nlme package; Pinheiro, Bates, Debroy, Sarkar, & R Core Team, 2016) that incorporated random effects accounting for variability from blocks (four paired plots). Variable selection was performed by a stepwise procedure minimizing the Akaike information criterion (MASS package; Venables & Ripley, 2002) and by checking for a consistent bias in normalized residuals (residuals divided by observed values). All computations were performed by RStudio (RStudio Team, 2016).

A natural logarithm transformation on both response and continuous predictor variables was applied for all allometric relationships. When estimates from the allometric relationships were back-transformed to the original scale (e.g., tree height, volume, and biomass), taking the exponential of the estimates creates bias because the transformation is nonlinear (Clifford, Cressie, England, Roxburgh, & Paul, 2013). A correction factor based on mean square error of the regression was therefore used to account for the bias with back transformation (Baskerville, 1972; Mascaro, Litton, Hughes, Uowolo, & Schnitzer, 2011).

3 | RESULTS

3.1 | Diameter and height relationships

We evaluated the effect of treatment on *H* and DBH for harvested trees following harvest. The average DBH and *H* of *P. taeda* in 2010 were 21.5 cm and 20.1 m in aCO_2 and 24.0 cm and 21.8 m in eCO_2, respectively. Both DBH and *H* of *P. taeda* were greater in eCO_2 than aCO_2 ($p < .0001$ for both DBH and *H*). The average DBH and *H* of broad-leaved species in eCO_2 (5.1 cm and 7.9 m, respectively) were also greater than those in aCO_2 (4.7 cm and 7.2 m; $p = .0178$ and .0059 for DBH and *H*, respectively).

We then evaluated the *H*–DBH allometry for harvested trees. For *P. taeda*, the relationship between DBH and *H* was well-described by log–log regression provided that we permitted treatment effects (Equation 2; $R^2 = .73$; Figure 1). The main effect of eCO_2 was significant ($p = .0003$). Overall, trees subjected to eCO_2 were ~5% taller at a given DBH than those in aCO_2 (Figure 1a; Tables S1 and S2). There were no effects of N fertilization or the interaction of CO_2 and N, on the DBH–*H* relationship ($p = .4109$ and .3482, respectively). For broad-leaved species in 2010, no treatment effect was observed ($p = .1684$, .0794, and .7297 for CO_2, N, and CO_2 × N, respectively; Figure 1b; Table S1), and a single log–log regression was defined that included trees from all treatments ($R^2 = .75$; Figure 1).

The DBH–*H* relationship of *P. taeda* changed over time. We derived treatment- and year-specific DBH–*H* relationships for years with *H* measurements available (Equation 1; 1996–1997, 2000–2001, 2004–2010), with selected regressions shown in Figure 2. We performed an analysis of covariance to determine whether the 2010 harvest-based regression differed from any of the pre-2010 regressions in intercept (β_{t1} in Equation 1), slope (β_{t2} in Equation 1), or both. For the aCO_2 plots, the scaling exponent (β_{t2} in Equation 1) of the 2010 harvest-based regression was significantly greater than the exponents derived from the 2000, 2004, and 2005 regressions ($p = .0364$, .0072, and .0344, respectively), but was smaller than that of regression in 2001 ($p = .0007$; Table S3). Under eCO_2, the scaling exponent derived from the harvest did not differ from those derived in any other year (Table S3). Under both aCO_2 and eCO_2, the intercept term (β_{t1} in Equation 1) increased with time (Table S3).

We then analyzed how the CO_2 treatment effect changed with time. We found a treatment effect on the slope in 2001 (greater scaling exponent in aCO_2), but not other years (Tables S1 and S4). A treatment effect on the intercept was found from 2000 onward (Table S4). We found no CO_2 treatment effect on DBH–*H* allometry in 1996–1997

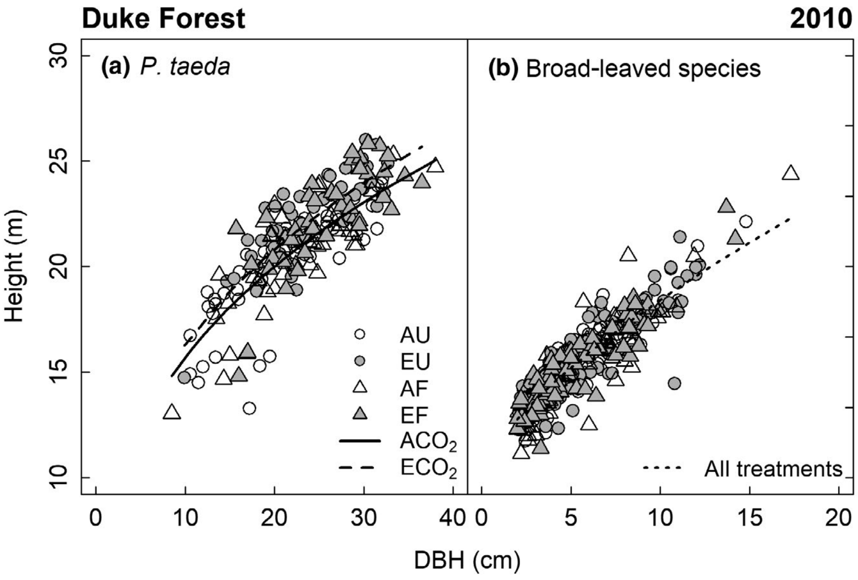

FIGURE 1 Tree height (*H*)–diameter at breast height (DBH) relationships for harvested *Pinus taeda* (a) and combined broad-leaved species (b). Symbols indicate treatment conditions: ambient CO_2 (aCO_2) unfertilized (AU: open circles); elevated CO_2 (eCO_2) unfertilized (EU: closed circles); aCO_2 N-fertilized (AF: open triangles); eCO_2 N-fertilized (EF: closed triangles). Solid, dashed, and dotted lines are regression lines

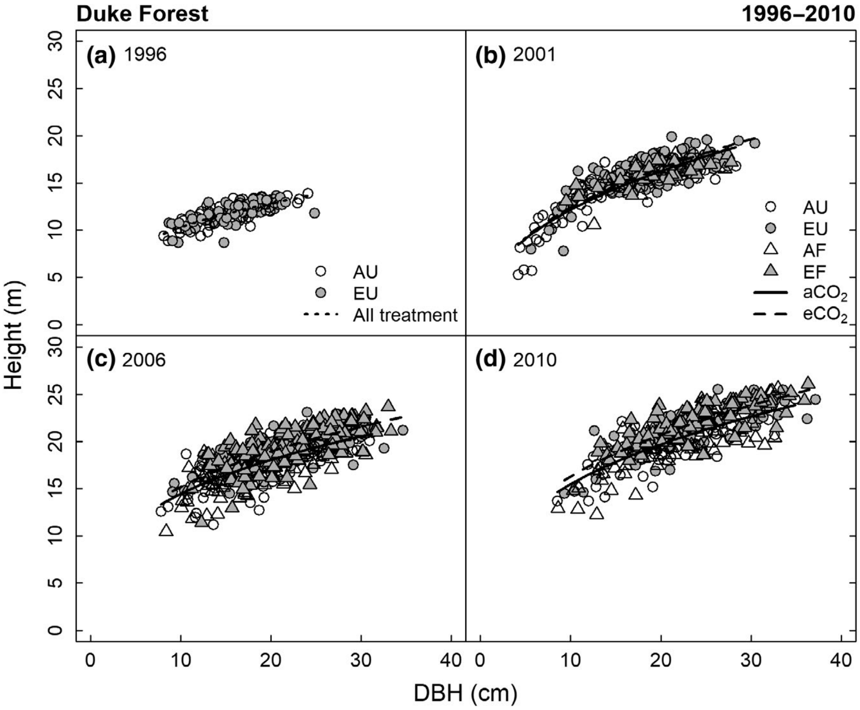

FIGURE 2 Relationships between diameter at breast height (DBH) and tree height (*H*) of *Pinus taeda* in 1996 (a), 2001 (b), 2006 (c), and 2010 (d). Symbols indicate treatment conditions: ambient CO_2 (aCO_2) unfertilized (AU: open circles); elevated CO_2 (eCO_2) unfertilized (EU: closed circles); aCO_2 N-fertilized (AF: open triangles); eCO_2 N-fertilized (EF: closed triangles). The solid and dashed lines are regression lines fitted to aCO_2 and eCO_2 data; the dotted line in (a) is a regression line fitted to all treatment data

(p = .4615 and .1338; Figure 2). However, as a result of the combined effects on slope and intercept, trees were ~2% taller in eCO_2 by 2000, and this effect persisted in 2001 and 2004 (p = .0381, .0051, and .0223, respectively). Trees were ~5% taller in eCO_2 in 2005–2010 (p < .0001 in 2005–2009 and p = .0016 in 2010; Figure 3; Table S1).

3.2 | Allometric equations for plant volume and biomass

The relationships between stem volume and DBH in aCO_2 and eCO_2 were different for *P. taeda*, but not for broad-leaved species. N fertilization did not change the relationships for any species. An allometric equation for *P. taeda* stem volume using only DBH as a predictor underestimated the stem volume of large trees in eCO_2 (Figure S2). This bias was removed when we included CO_2 treatment and an interaction term (DBH × CO_2) in the equation (Figure 4a; Figure S2; Table S1). Neither N fertilization nor CO_2 × N interaction effects on the relationship were observed (p = .3146 and .7713). Alternatively, when *H* and its corresponding interaction terms were added as additional predictor variables in the equation for stem volume, the effect of CO_2 disappeared (Table S1). For broad-leaved species, effects of CO_2, N, and CO_2 × N were not observed regardless of whether DBH alone or both DBH and

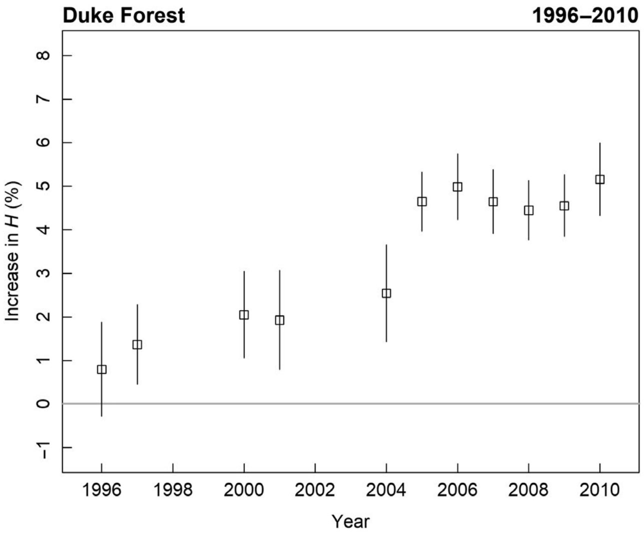

FIGURE 3 Effect of eCO_2 on tree height (H) based on year-specific relationship between diameter at breast height (DBH) and H of *Pinus taeda*. A gray horizontal line indicates zero. Vertical bars indicate 1 *SE*

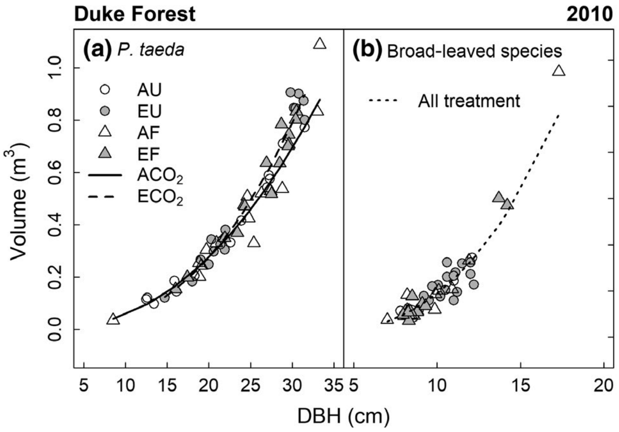

FIGURE 4 Stem volume of *Pinus taeda* (a) and combined broad-leaved species (b) versus diameter at breast height. Symbols indicate treatment conditions: ambient CO_2 (aCO_2) unfertilized (AU: open circles); elevated CO_2 (eCO_2) unfertilized (EU: closed circles); aCO_2 N-fertilized (AF: open triangles); eCO_2 N-fertilized (EF: closed triangles). The solid and dashed lines in (a) are regression lines fitted to aCO_2 and eCO_2 data; the dotted line in (b) is a regression line fitted to all treatment data

H were included in the model (p = .9743, .9671, and .8555 with DBH alone and p = .7432, .6080, and .8150 with both DBH and H; Figure 4b; Table S1). Neither did any CO_2 or N effect emerge when we derived separate allometric equations with both DBH and H for stem wood and stem bark volume (Figure S3; Table S2). No significant bias or patterns were observed in the normalized residuals of the regression models (Figure S4; Table S2). The ranges of DBH and H of trees used to develop the allometric equations were 8.5–33.3 cm and 13.1–26.0 m for *P. taeda* and 7.0–17.3 cm and 6.7–21.6 m for broad-leaved species, respectively.

Wood and bark densities of stem disks changed with the distance of stem disk from tree top, but not with eCO_2 or N fertilization. When wood and bark densities at breast height were assumed as average values of a tree, H difference of *P. taeda* in eCO_2 led to slight differences in the density estimates. Wood density of stem disks increased with distance from tree top (p < .0001 for *P. taeda* and p = .0203 for *L. styraciflua*; Figure 5a,b), but bark density decreased (p = .0002 and .0001; Figure 5d,e). The relationships between wood and bark densities of stem disk and the distance of stem disk from tree top did not differ by CO_2 or N treatment (Figure 5). However, due to H differences between aCO_2 and eCO_2, the average stem wood and stem bark densities at breast height (1.3 m from the ground) in 2010 were 2.4% higher and 3.9% lower in eCO_2, respectively than those in aCO_2 (p < .0001; Figure 5c,f). N fertilization did not affect the average stem wood and stem bark densities at breast height (p = .4540). Stem wood and stem bark densities at breast height of *L. styraciflua* were similar under all treatments (p = .1140 and .5090 for CO_2 and N, respectively). The relationships for broad-leaved species other than *L. styraciflua* were not tested due to small sample sizes.

Elevated CO_2 changed the relationship between stem biomass and DBH, indicating a change in allometry such that eCO_2 plants had higher stem biomass for the same DBH. When H was incorporated into the relationships, eCO_2 was no longer a significant predictor. Allometric equations for tree-level stem, branch, and foliage biomass of *P. taeda* and combined broad-leaved species were developed considering DBH, CO_2, and N treatment as predictors (Equations 7 and 9; Figure 6; Table S2). For *P. taeda*, stem biomass at a given DBH in eCO_2 was greater than that in aCO_2 when DBH >20 cm (p = .0042 for the interaction of DBH and CO_2). At a given DBH, branch biomass decreased (p = .0057) and foliage biomass did not change in eCO_2 (p = .2540), which indicates a greater foliage biomass per unit branch biomass of a tree in eCO_2 than that of a tree in aCO_2 with the same DBH. The relationship between stem biomass and DBH of *P. taeda* in aCO_2 and eCO_2 was not different if H was added in the model (p = .0307 for DBH × H and p = .8614 for CO_2; green line in Figure 6a). In an alternative model for branch biomass of *P. taeda* with CL and BAP (p = .0230 and .0058), the CO_2 treatment effect was not significant (p = .0779; Figure 6c). N fertilization did not change the relationships for any component of *P. taeda*. For combined broad-leaved species, the relationships for stem biomass and branch biomass were unaffected by either CO_2 or N treatment (Figure 6b,d). Adding H or ST improved the models (R^2 = .91 and .69 for stem and branch biomass, respectively; Figure S5; Table S2).

3.3 | Stand-level aboveground biomass

Elevated CO_2 increased standing aboveground biomass of *P. taeda*, but did not change that of broad-leaved species. The aboveground biomass of *P. taeda* in EU, which was not different from that in AU in 1996 (p = .7802; Figure 7a), became greater than that in AU from 2003 onward (p = .0312). The aboveground biomass difference between pretreatment and end-of-treatment of *P. taeda* in EU was greater by 46.2% than that in AU (7,724 and 11,292 g C/m^2 in AU and EU, respectively). This caused

31.2% greater aboveground biomass of *P. taeda* in EU than AU in 2010 (p = .0111; Figure 7b). For broad-leaved species, eCO_2 did not affect the aboveground biomass in any year ($p \geq .1577$; Figure 7c). Similar to *P. taeda* biomass, eCO_2 differentiated stand-level aboveground biomass in AU and EU since 2003 (p = .0285; Figure 7e), ultimately leading 30.8% greater stand-level aboveground biomass in 2010 (Figure 7).

N amendment for 6 years did not change standing aboveground biomass of either *P. taeda* or broad-leaved species. For the *P. taeda* trees which received N fertilization from 2005 to 2010, the effect of N fertilization was not observed in either aCO_2 or eCO_2 conditions (Figure 7). N fertilization did not change the biomass of broad-leaved species (in total and by component) in either aCO_2 or eCO_2 (Figure 7). For stand-level biomass, the aboveground biomass in eCO_2 N-fertilized (EF) were not different from that in EU ($p \geq .3387$). A difference in biomass between AU and aCO_2 N-fertilized (AF) was found only in 2005 (p = .0349).

Stem biomass of *P. taeda* in this study was greater than that would have been estimated following approaches in a previous study (Figure S6; McCarthy et al., 2010). When stem wood and stem bark densities were assumed to be fixed (0.427 and 0.279 g/cm^3; Naidu et al., 1998), the stem biomass in this study was 12.7% and 10.5% greater than estimates from the previous approach in 1996. The difference disappeared at the later period of the experiment. With new estimates of stem wood and stem bark densities, the stem biomass in this study was 15.7%–37.9% greater than that from the previous approach (Figure S6b).

Finally, we partitioned the effect of CO_2 on *P. taeda* biomass into four components: rate of diameter growth, change in stem allometry, rate of foliar growth, and rate of branch growth. To compute the pure effect of faster diameter growth, we re-computed the biomass in the eCO_2 plots using allometries derived from the aCO_2 plots. This procedure led to approximately 20% (23.1 ± 6.0%

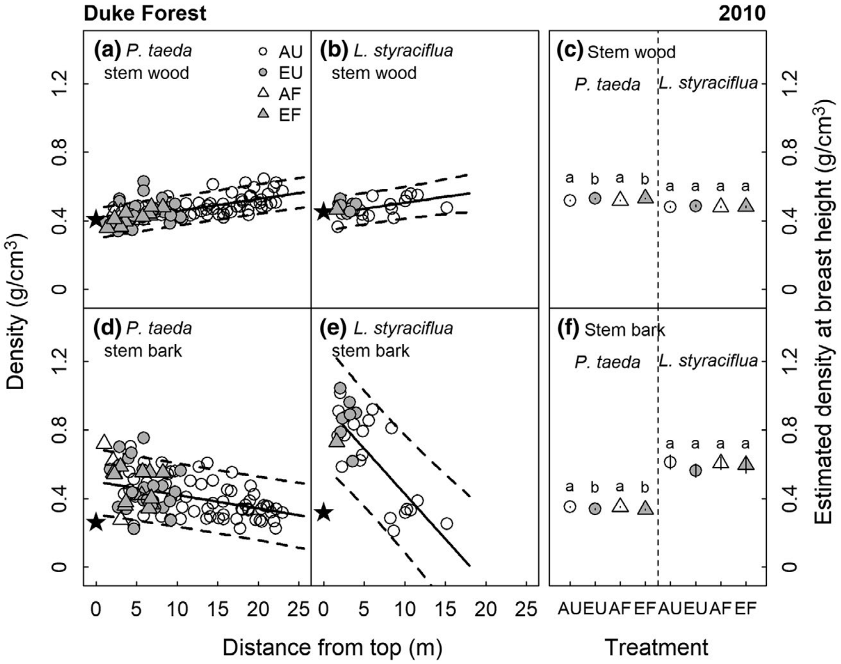

FIGURE 5 Relationship between distance from tree top and densities of stem wood and stem bark of *Pinus taeda* (a, d) and *Liquidambar styraciflua* (b, e). Symbols indicate treatment conditions: ambient CO_2 (aCO_2) unfertilized (AU: open circles); elevated CO_2 (eCO_2) unfertilized (EU: closed circles); aCO_2 N-fertilized (AF: open triangles); eCO_2 N-fertilized (EF: closed triangles). For EU, AF, and EF, only stem disks which were developed after the treatment was initiated were included. Solid and dashed lines indicate fitted values and 95% prediction intervals under AU condition. Stars in (a), (b), (d), and (e) indicate average densities used in McCarthy et al. (2010). In (c) and (f), densities of stem wood and stem bark at breast height were estimated based on tree height survey data in 2010

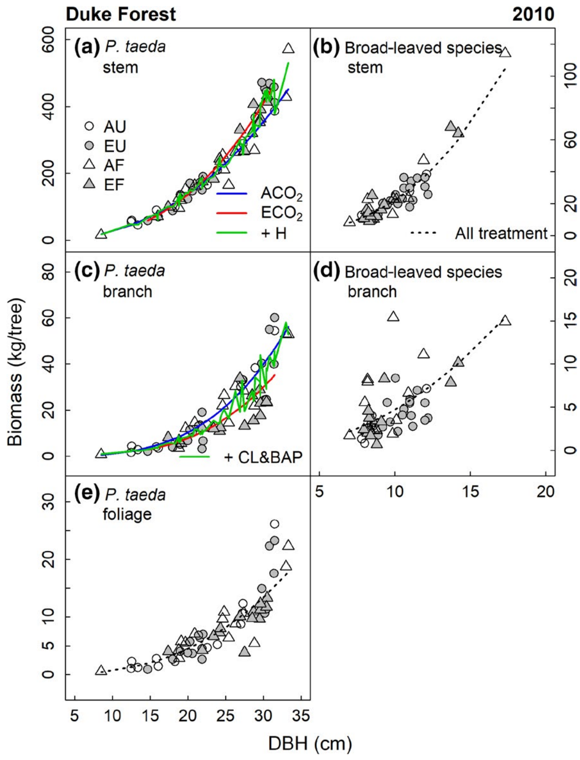

FIGURE 6 Biomass of stem (a, b), branch (c, d), and foliage (e) of *Pinus taeda* (left panels) and combined broad-leaved species (right panels) versus diameter at breast height (DBH). Symbols indicate treatment conditions: ambient CO_2 (aCO_2) unfertilized (AU: open circles); elevated CO_2 (eCO_2) unfertilized (EU: closed circles); aCO_2 N-fertilized (AF: open triangles); eCO_2 N-fertilized (EF: closed triangles). Blue and red solid lines are regression lines fitted to aCO_2 and eCO_2 data; black-dotted lines are regression lines fitted to all treatment data. Green solid lines in (a) and (c) are jagged because the regressions include multiple predictors (DBH + tree height or DBH + CL + BAP). BAP, basal area percentile; CL, crown length [Colour figure can be viewed at wileyonlinelibrary.com]

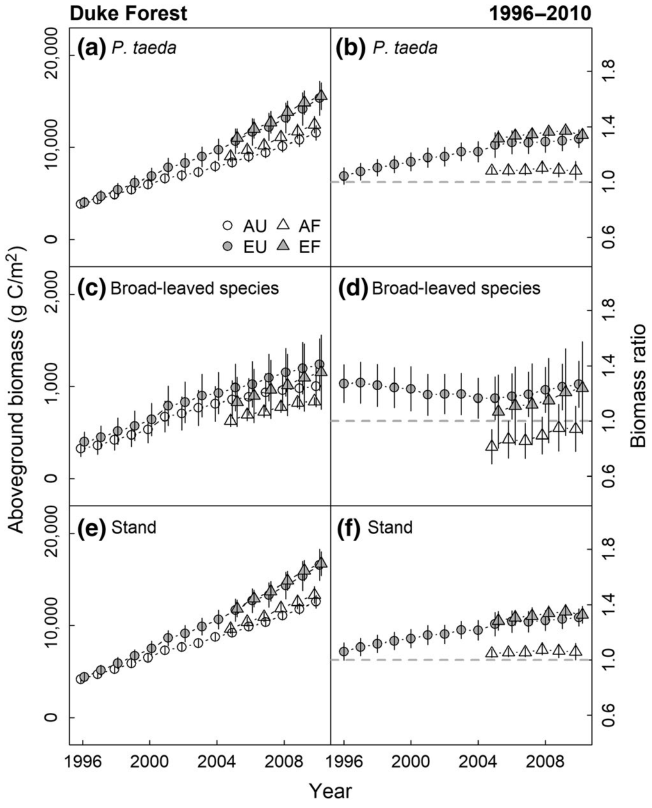

FIGURE 7 Aboveground biomass of *Pinus taeda* (a), combined broad-leaved species (c), and stand total (e) under ambient CO_2 (aCO_2) unfertilized (AU: open circles), elevated CO_2 (eCO_2) unfertilized (EU: closed circles), aCO_2 N-fertilized (AF: open triangles), and eCO_2 N-fertilized (EF: closed triangles) conditions and ratio of biomass under EU, AF, and EF to that under AU (b, d, f). Vertical bars indicate 1 *SE*

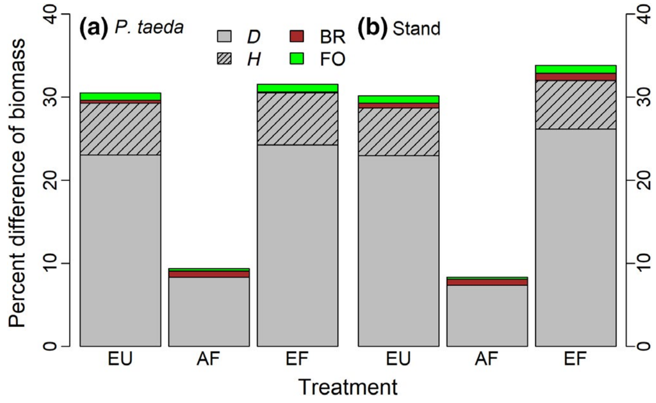

FIGURE 8 Percent difference of aboveground biomass of *Pinus taeda* (a) and stand total (b) in 2010 under elevated CO_2 (eCO_2) unfertilized (EU), ambient CO_2 (aCO_2) N-fertilized (AF), and eCO_2 N-fertilized (EF) against the biomass under aCO_2 unfertilized (AU). Each stacked bar indicates difference of biomass caused by differences of diameter (*D*), height (*H*), branch biomass (BR), and foliage biomass (FO) [Colour figure can be viewed at wileyonlinelibrary.com]

between EU and AU, and 16.2 ± 4.4% between EF and AF; Figure 8) greater aboveground biomass in eCO_2 plots than those in aCO_2 plots at the end of the experiment due to increase of stem biomass. Adding the effect of CO_2 on stem allometry resulted in an additional 6% (6.3 ± 0.4% between EU and AU, and 5.8 ± 0.2% between EF and AF) difference of biomass. Foliar growth caused 0.7 ± 0.1% differences of biomass between eCO_2 and aCO_2. No significant difference in branch biomass was found (p = .7468; Figure 8a). Comparison of the AU and EF treatments led to similar results to that between AU and EU (Figure 8a). Differences in stand-level biomass in EU, AF, and EF compare to values in AU were similar to those of *P. taeda* (Figure 8b).

4 | DISCUSSION

We found that *P. taeda* trees had a greater *H* at a given DBH in eCO_2, but broad-leaved species did not. This treatment effect arose through both through changes in the allometric intercept term (Equation 1; 2000–2010) and in the allometric exponent (2001). The allometric relationships between DBH and stem volume and between DBH and stem biomass of *P. taeda* in eCO_2 were different from those in aCO_2, but these differences disappeared when both *H* and DBH were used as predictors. Vertical variations of stem wood and stem bark densities of *P. taeda* were unaffected by either CO_2 or N. eCO_2 reduced branch biomass of *P. taeda* at a given DBH, but did not change foliage biomass. The effect of N was not observed in any allometric equations for all species. eCO_2 increased stand-level standing aboveground biomass, but the effect of N fertilization was limited to the first year of fertilizer application in aCO_2 condition.

4.1 | Effects of CO_2 enrichment and N amendment on diameter-height allometry

In contrast to some previous FACE studies (DeLucia et al., 2002; McCarthy et al., 2010), we found that *H* at a given DBH was greater in eCO_2 than in aCO_2 for *P. taeda* (Figure 1), which supports our first hypothesis (H1: positive CO_2 effects on *H* at a given DBH). One possible explanation for our result is that we used a longer time series than previous studies. Given that all of our trees experienced aCO_2 conditions from the seedling stage to an age of 15 years, it is perhaps unsurprising that an extended period of exposure to eCO_2 was required before a significant difference emerged. However, the minimum experimental duration required to observe a CO_2 effect on DBH–*H* allometry may vary with ontogeny. For example, our results are in accordance with observations of *P. taeda* seedlings grown in open-top chambers, where changes in plant architecture (e.g., increases in tree height and branch number per unit tree height) in eCO_2 were observed after 19 months (Tissue, Thomas, & Strain, 1996, 1997).

Our study helps address the question of whether the effect of eCO_2 on allometry is similar to an acceleration of stand development (Hasegawa et al., 2018; Körner, 2006; Pretzsch et al., 2014). Our results mostly support this idea. eCO_2 resulted in taller trees for a given DBH (Figure 1), similar to how trees are taller for a given DBH in older stands than in younger stands (Lappi, 1997; McCarthy et al., 2010; Sumida et al., 2013). Furthermore, aging and eCO_2 both increased the intercept term in Equation (1) without changing the scaling exponent in years 11–15 of the experiment (2006–2010), resulting in greater *H* at a given DBH (Figure 2; Figure S1; Tables S3 and S4). In contrast, stand aging and eCO_2 treatment had inconsistent effects on the allometric scaling component during years 5–10 of the experiment (2000–2005; Tables S3 and S4). Because much fewer trees had *H* measurements before 2005 (30.0% and 98.7% before and after 2005, respectively), the pre-2005 changes in allometry should be interpreted with caution.

4.2 | Treatment effects on allometric relationships for tree biomass estimation

We found that the allometric equations for both stem volume and stem biomass of *P. taeda* were affected by CO_2 enrichment when DBH was the only predictor variable (Figures 4 and 6), but not when *H* was included as an additional predictor variable (Figure 6a). This result suggests that the difference in allometry for stem volume or stem biomass by CO_2 treatment is due to changes in tree geometry (i.e., DBH–*H* relationship) in eCO_2 (Tissue, Thomas, & Strain, 1997). Lack of eCO_2 effect for broad-leaved species was consistent with previous studies. Norby et al. (2001) did not find changes in *H* or taper index (based on ratio of cross-sectional area at 1.3 and 4.0 m from ground) in eCO_2, which were considered to alter the allometric relationships between basal area and tree volume of *L. styraciflua*. No CO_2 effects on allometric equations with basal area were observed in poplar plantations (Calfapietra et al., 2003; Liberloo et al., 2006). However, it should be noted that these studies were based on measurements after 1–3 years of CO_2 enrichment, which may be too short to induce structural differences.

As the distance from tree top to a stem disk sample increased, we found that stem wood density increased and stem bark density decreased for both *P. taeda* and *L. styraciflua* (Figure 5). Combining the wood and bark components, stem density of *P. taeda* increased with the distance from top while those of *L. styraciflua* decreased due to a greater bark volume fraction to stem volume (19.4% on average) and large changes in stem bark density with locations (Figure S9). We found no effect of CO_2 or N on the vertical variation of wood and bark densities in *P. taeda*. However, the larger *H* at a given DBH in eCO_2 allowed a slightly higher tree-level stem wood density and a slightly lower stem bark density for *P. taeda* in aCO_2 (Figure 5c,f). Our results are consistent with earlier analyses of the responses of wood and bark densities of 12-year-old *P. taeda* branches to eCO_2 (Murthy & Dougherty, 1997). Similarly, Telewski et al. (1999) did not find a significant effect of eCO_2 on maximum latewood (excluding 1 year), minimum earlywood, and average wood densities of *P. taeda* in an OTC experiment over 4 years. Consistent with our study, Norby et al. (2001) did not observed significant changes in wood density of *L. styraciflua* stem core samples during 3 years of CO_2 enrichment.

Because harvest occurred only in a single year, we were unable to assess the effect of tree age (or stand age) on stem wood or stem bark densities. However, previous studies have reported that whole-core density at breast height and stem average density of *P. taeda* increases as trees mature (Albaugh, Allen, Dougherty, & Johnsen, 2004; Jordan, Clark, Schimleck, Hall, & Daniels, 2008; Lenhart, Shinn, & Cutter, 1977; Taylor & Burton, 1982), which make it inappropriate to use a constant wood or bark density for long-term estimations of tree biomass. Taylor and Burton (1982) observed that stem density of *P. taeda* stem increased from 0.40 to 0.52 as the stand aged from 10 to 35 years old. Our approach of determining tree-level stem density (i.e., stem wood and stem bark densities at breast height) based on the relationship between density of stem disk and the location of the disk along the stem estimated values within ranges at similar ages (Jordan et al., 2008; Taylor & Burton, 1982), and it is consistent with the previously observed increase in stem density of the stem with age (Albaugh et al., 2004; Jordan et al., 2008; Lenhart et al., 1977; Taylor & Burton, 1982).

Stem biomass estimates in this study were greater than that would have been estimated following approaches in a previous study at the same site (Figure S6; McCarthy et al., 2010). While the difference due to use of a different DBH–*H* relationship in gap filling and to use of new parameters in the allometric equation for stem volume was largest in the earlier part of the time series, the difference due to stem wood and stem bark densities was largest in later years of experiment. Because stem volume measurements in earlier years were not available, we could not confirm which volume estimates are more accurate. If the allometric equation for stem volume is different for different tree ages (Fatemi et al., 2011), then the stem biomass from Fang et al. (2000) might be more accurate in the earlier years of stand development, when tree ages were closer to the ages of the trees that the equation was based on (14 years old on average; ranged 9–26 years old). If the parameters were not sensitive to tree age (Crow, 1983), the estimates from the site-specific equation in this study would be more accurate. In later years, because *H* of most trees was measured (99.2% in 2009) and stem volumes from the two allometric equations agreed well (Figure S8), the differences in stem biomass were likely to be almost entirely from our parameterization of stem wood and stem bark densities. The stem densities in the last year of this study (0.527 and 0.341 g/cm^3 for stem wood and stem bark) were greater than those from a previous study from this and nearby stands (0.427 and 0.279 g/cm^3; Naidu et al., 1998), and it is likely because our sample trees were older (30 years old) than the trees used in the earlier study (18.9 years old on average; ~87% 10–18 years old). Our results indicate that use of a constant wood and bark densities based on estimates from young trees would cause a large and growing underestimation in stem biomass and stand-level biomass in a maturing forest.

Branch biomass of a tree in eCO_2 was predicted to be smaller than that of a tree with the same DBH in aCO_2 (Figure 6c). When CL and BAP were added as additional variables, the effect of eCO_2 was not significant (Figure 6c; Table S2). These results suggest that the

CO_2 effects may be due to changes in CL and social status of trees in eCO_2. The negative effects of eCO_2 on branch biomass suggest that the proportion of branch biomass to stem biomass is reduced in eCO_2 with variations depending on tree diameter. Calfapietra et al. (2003) observed a decrease in branch-to-stem biomass ratio for *P. alba*, but the ratio did not change for *P. nigra*. Although the CO_2 effect on the biomass proportion among aboveground components were not observed for *P. taeda* (McCarthy et al., 2010; Tissue et al., 1997), changes in proportion of standing biomass of stem (increase) and foliage (decrease) with time (or stand development) were observed (McCarthy et al., 2010). This suggests that the reduced proportion of branch biomass might be because the trees in eCO_2 were in more advanced stage of the stand development. It is also possible that the reduced proportions of branch biomass were because a tree in eCO_2 with the same DBH as a tree in aCO_2 would be more suppressed, thus presenting a greater need for allocation to stem height growth (Kunz et al., 2019; Naidu et al., 1998).

4.3 | Treatment-induced changes in aboveground biomass

We found that *P. taeda* aboveground biomass were greater in eCO_2 than in aCO_2 throughout the second half of our experiment (2003–2010; Figure 7). Whereas the aboveground biomass difference between eCO_2 and aCO_2 was 22.8% in 2004 (Finzi et al., 2006; McCarthy et al., 2010), it reached ~27% by 2010 (Figure 7b). Unlike *P. taeda*, the biomass of broad-leaved species in eCO_2 was not different from that in aCO_2 at any point during our study period (Figure 7; Kim et al., 2016; McCarthy et al., 2010). The lack of response may indicate the compensation of expected growth-enhancing effect of eCO_2 and reduced light due to higher leaf area of the dominant species since the early period of experiment (Kim et al., 2016; McCarthy et al., 2007; Walker et al., 2019).

The greater *H* at a given DBH (and corresponding increase of stem volume) of *P. taeda* in eCO_2 was responsible for ~6% out of ~27% difference of *P. taeda* biomass between aCO_2 and eCO_2 at the last year of the treatment (Figures 1 and 8). Thus, the effect of CO_2 on the *P. taeda* biomass and stand-level biomass would be underestimated without correcting the CO_2-related changes in DBH–*H* relationship of *P. taeda*, supporting H2 (underprediction of biomass without accounting for increased *H* under eCO_2). Because it took ~9 years for the DBH–*H* relationship of *P. taeda* in eCO_2 to diverge from that in aCO_2, our biomass estimates differ only modestly from early estimates of biomass production and standing biomass at the site (DeLucia et al., 1999, 2002; Hamilton et al., 2002; McCarthy et al., 2010; Schäfer et al., 2003). However, the DBH–*H* relationship in eCO_2 is critical to accurate estimation of biomass both during the later years of the experiment and presumably under future conditions.

Against our expectations (H3; positive effect of N fertilization on biomass) and with other N fertilization studies (Borders et al., 2004; King et al., 2008; Menge et al., 1977), during 6 years of N amendment, we found no differences of biomass between AU and AF, and between EU and EF (Figure 7). These results are inconsistent with the findings that fertilization enhanced annual carbon increments in woody tissue (including a synergistic effect with CO_2 and fertilization) and NPP of the prototype plot and its reference plot (McCarthy et al., 2010; Oren et al., 2001). The difference in response may be because the prototype and reference plots had received a complete fertilization annually, depending on the nutrient requirements for that year (Albaugh et al., 1998; Linder, 1995), while the other six plots had received N fertilization only. Our inability to discern an N effect, together with the sustained effect of eCO_2 on biomass, suggests that progressive N limitation (Luo et al., 2004; Norby, Wullschleger, Gunderson, Johnson, & Ceulemans, 1999) was not observed at this site during 15-year CO_2 enrichment. In eCO_2, increased carbon flux belowground via litterfall (Lichter et al., 2008), fine root biomass (Jackson, Cook, Pippen, & Palmer, 2009; Matamala & Schlesinger, 2000; Pritchard, Strand, McCormack, Davis, Finzi, et al., 2008), root exudation (Phillips, Finzi, & Bernhardt, 2011), and ectomycorrhizal production (Drake et al., 2011; Pritchard, Strand, McCormack, Davis, & Oren, 2008; Talbot, Allison, & Treseder, 2008; Terrer et al., 2018) may have stimulated microbial soil organic matter (SOM) decomposition, and thus enhanced N uptake of trees from SOM (Drake et al., 2011; Palmroth et al., 2006; Phillips et al., 2011). With N fertilization, trees in eCO_2 did not increase root exudation or fine root biomass (Jackson et al., 2009; Phillips et al., 2011), which may reduce the turnover rate of SOM, but did not cause a notable difference in aboveground biomass.

Over the last several decades, atmospheric CO_2 enrichment experiments on forest ecosystems have shown that forests respond to eCO_2 in various ways. While some can occur relatively quickly (e.g., leaf-level photosynthesis and stomatal conductance), others may require longer periods (e.g., biomass accumulation and community composition). Given the size of the effect that we report, allometry changes should be considered when computing biomass under elevated atmospheric CO_2 concentrations. We did not observe similar responses from combined broad-leaved species, but they were regenerated at different times of the experiment, they were typically suppressed, and data were more limited simply because they were not the dominant component at our study site. Thus, further observations are needed to determine the extent to which other species experience allometric changes under eCO_2.

ACKNOWLEDGEMENTS

We thank the numerous graduate students, technicians and collaborators who contributed to the harvest processes at the Duke FACE site. We would also like to thank Ram Oren and three anonymous reviewers for insightful comments. This research was supported in part by the Office of Science (BER) of the US Department of Energy through the Southeastern Regional Center (SERC) of the National Institute for Global Environmental Change (NIGEC), through the Terrestrial Carbon Processes (TCP) program, and by the US Forest Service Southern Research Station.

DATA AVAILABILITY STATEMENT

All data necessary to reproduce our analyses are openly available in a GitHub repository at https://github.com/kein1331/FACE_allometry/.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Kim D, Medvigy D, Maier CA, Johnsen K, Palmroth S. Biomass increases attributed to both faster tree growth and altered allometric relationships under long-term carbon dioxide enrichment at a temperate forest. *Glob Change Biol*. 2020;26:2519–2533. https://doi.org/10.1111/gcb.14971