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RESEARCH ARTICLE

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Getting allometry right at the Oak Ridge free-air CO_2 enrichment experiment: Old problems and new opportunities for global change experiments

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Societal Impact Statement

Free-air CO_2 enrichment (FACE) experiments provide essential data on forest responses to increasing atmospheric CO_2 for evaluations of climate change impacts on humanity. Understanding and reducing the uncertainty in the experimental results is critical to ensure scientific and public confidence in the models and policy initiatives that derive therefrom. One source of uncertainty is the estimation of tree biomass using mathematical relationships between biomass and easily obtained and non-destructive measurements (allometry). We evaluated the robustness of the allometric relationships established at the beginning of a FACE experiment and discuss the challenges and opportunities for the new generation of FACE experiments.

Summary

- Long-term field experiments to elucidate forest responses to rising atmospheric CO_2 concentration require allometric equations to estimate tree biomass from non-destructive measurements of tree size. We analyzed whether the allometric equations established at the beginning of a free-air CO_2 enrichment (FACE) experiment in a *Liquidambar styraciflua* plantation were still valid at the end of the 12 year experiment.
- Aboveground woody biomass was initially predicted by an equation that included bole diameter, taper, and height, assuming that including taper and height as predictors would accommodate changes in tree structure that might occur over time and in response to elevated CO_2. At the conclusion of the FACE experiment, we harvested 23 trees, measured dimensions and dry mass of boles and branches, and extracted and measured the woody root mass of 10 trees.
- Although 10 of the harvested trees were larger than the trees used to establish the allometric relationship, measured aboveground woody biomass was well predicted by the original allometry. The initial linear equation between bole basal area and woody root biomass underestimated final root biomass by 28%, but root

[†] This paper is dedicated to the memory of our colleague and friend Joanne Childs, whose technical support was instrumental throughout this FACE experiment.

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biomass was just 21% of total wood mass, and errors in aboveground and belowground estimates were offsetting.

- The allometry established at the beginning of the experiment provided valid predictions of tree biomass throughout the experiment. New allometric approaches using terrestrial laser scanning should reduce an important source of uncertainty in decade-long forest experiments and in assessments of centuries-long forest biomass accretion used in evaluating carbon offsets and climate mitigation.

KEYWORDS
allometry, free-air CO_2 enrichment (FACE), *Liquidambar styraciflua*, root biomass, tree biomass

1 | INTRODUCTION

Accurate estimates of forest carbon stocks, and how they will change over time in response to climate change and rising atmospheric CO_2 concentration, are critical to climate change mitigation efforts (Anderegg et al., 2020; Demol et al., 2022; Stovall et al., 2018; Temesgen et al., 2015; Walker et al., 2021). Earth system models that project future climate change vary considerably on the size of the feedback between terrestrial vegetation and the atmosphere, and the response of forests to elevated CO_2 (eCO_2) is a major uncertainty in that interaction (Medlyn et al., 2015). Free-air CO_2 enrichment (FACE) experiments provide data and insights on forest responses to eCO_2 that can inform models and policy decisions on mitigation efforts. Most efforts to quantify forest biomass, carbon stocks, or biomass accretion, whether in national carbon stock assessments (Calders et al., 2022; Temesgen et al., 2015) or in FACE experiments, require the use of allometric equations to relate easily measured and non-destructive metrics, particularly diameter at breast height (DBH) and tree height (H), to dry woody mass (Picard et al., 2015; Stovall et al., 2023). The alternative approach of felling, sectioning, and weighing the trees at the site of interest is difficult, labor intensive, and expensive, and it may be precluded due to inaccessibility, site conservation, or maintenance of experimental integrity (Stovall et al., 2018).

Allometry has been widely used in forest FACE experiments as the primary method for evaluating the effects of eCO_2 on tree growth (Ellsworth et al., 2017; King et al., 2005; McCarthy et al., 2010; Talhelm et al., 2014). The allometric equation used, however, may have been established in a forest stand of different age and size structure, and allometric relationships can change with tree ontogeny and environmental influences (King et al., 1999; Temesgen et al., 2015), including atmospheric and climatic change. Hence, an important and unknown element of uncertainty can be introduced in biomass and growth estimates. The problem will be particularly acute for the AmazonFACE experiment in a highly diverse tropical rainforest (Norby et al., 2016). Standard allometry can lead to large uncertainty with large trees (Calders et al., 2015), and the very high diversity of tree species in the AmazonFACE experimental plots necessitates a reliance on equations constructed for generic tropical trees, made species-specific only with the inclusion of wood density in the equation (Chave et al., 2005). Furthermore, published equations developed by different researchers yield different estimates of tree aboveground biomass (AGB) at AmazonFACE (Pereira et al., 2019). The uncertainty introduced by the reliance on allometric equations also applies to national assessments of forest inventory and commitments to carbon credits. For example, Calders et al. (2022) showed that the allometry used in assessments of forest carbon stocks across Great Britain was seriously underestimating biomass compared to a newer and more reliable approach of direct, non-destructive measurements of tree volume using terrestrial laser scanning (TLS).

The Oak Ridge National Laboratory FACE (ORNL FACE) experiment reported tree biomass increment and net primary productivity (NPP) throughout the 12 year experiment (Norby et al., 2010) based on allometric equations for AGB and coarse root mass established at the beginning of the experiment. AGB and NPP initially increased in response to CO_2 enrichment, but the enhancement was gradually lost because of a nitrogen limitation. These results have been used as a benchmark for ecosystem models (Haverd et al., 2020; Hickler et al., 2008; Matthews, 2007) and to inform model development (Medlyn et al., 2015), so it is important that we have confidence in the data. Unlike some similar experiments, we had the opportunity to measure trees that were felled during the construction of the experimental infrastructure (Norby et al., 2001). This provided the advantage of using an allometry based on trees from the same population and site. However, since additional tree harvesting was precluded once the experiment started, we did not know whether the eCO_2 treatment would alter the DBH-mass relationship, or whether the relationship would change as the experimental trees grew larger than the trees in the calibration data set. In the DukeFACE experiment, the initial allometry established between DBH and volume and dry mass (Naidu et al., 1998) was later shown to be underestimating AGB because the DBH-H relationship changed during stand development, altering the allometric relationship and requiring a reassessment of the effects of eCO_2 on tree growth (McCarthy et al., 2010). With similar concerns in mind (and as described below), we included additional terms (H and taper [T]) in our allometric equation that might be affected by either eCO_2 or tree ontogeny and alter the relationship between DBH (or basal cross-sectional area) and biomass (Norby

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et al., 2001). An adjustment for relative changes in wood density was applied to the resulting prediction. These additional terms improved the precision of the estimates of woody biomass compared to the otherwise acceptable relation with DBH alone, but with the cost of additional measurements that needed to be made and the uncertainty associated with those more difficult measurements. H and T could not be measured on every tree; hence, mean values per plot were used in prediction equations.

When the experiment was terminated in 2009, we harvested a subset of experimental trees from ambient (aCO_2) and eCO_2 treatments with the objective of determining whether the allometric relations used to evaluate effects of eCO_2 on tree growth remained valid throughout the experiment. While we focus in this study on above- and belowground woody biomass, the harvest of trees also provided detailed information on leaf area and canopy structure (Norby et al., 2022), and soil pits dug at the same time provided detailed information of fine-root mass and soil carbon (Iversen et al., 2012). In the current study, our hypothesis is that by including terms in the allometric equation for estimating AGB that might change during ontogenetic development or in response to eCO_2, the equation would remain valid despite the limitations of the initial calibration data set. If the alternative hypothesis is true and the allometric equations did not remain valid, a reassessment and correction of our previous reports on responses to eCO_2 in this experiment would be necessary.

2 | METHODS

The ORNL FACE experiment was initiated in 1997 in a 1.3 ha *Liquidambar styraciflua* L. plantation (2.3 m × 1.2 m spacing) that had been established 9 years earlier on the Oak Ridge National Environmental Research Park in Tennessee, USA (35°54′N, 84°20′W). Five 25 m diameter plots were laid out, and elevated CO_2 treatments began in May 1998 and continued during the growing season (April through October) for 12 years. The average daytime (CO_2) near the top of the canopy over the duration of the experiment was 547 ppm in two eCO_2 plots and 395 ppm in three aCO_2 plots. Additional details of the experimental design, CO_2 exposure dynamics, stand structure, and site conditions have been provided elsewhere (Norby et al., 2001; https://richnorby.org/home/face-home/), and data on meteorological conditions and biological responses are publicly available (https://data.ess-dive.lbl.gov/).

When the FACE infrastructure was assembled in 1996, eight trees were cut down, measured, and sampled for determination of AGB (Norby et al., 2001) and leaf mass distribution (Norby et al., 2022). In 1999, after CO_2 treatments had been initiated, 10 additional trees were harvested from areas of the plantation outside of the treatment rings. In addition to the aboveground measurements, the coarse woody root systems of these trees were excavated using a power winch and hand tools. The roots were washed free of soil with a high-pressure hose, oven-dried, and weighed.

We developed and tested four different allometric equations expressing AGB as functions of different combinations of basal area (BA), total H, and T (Norby et al., 2001). Including all three terms improved the coefficient of determination (r^2) from 0.91 for the equation based only on BA to 0.97 and met our objective of including terms that might be expected to alter the relationship between BA and AGB during the course of the experiment. The best allometric relationship for AGB resulting from these data was

$$M_{AGB} = 30.25 + 0.0174 \times A_{1.3} \times H - 56.81 \times T; \; n = 18, r^2 = 0.97 \quad (1)$$

where M_{AGB} is aboveground woody dry mass (kg), $A_{1.3}$ is BA (cm^2), or cross-sectional area at 1.3 m height, H is total tree height (m), and T is taper index, defined as $1 - A_4 / A_{1.3}$, with A_4 being cross-sectional area at 4 m height (Norby et al., 2001). BA is equal to $\pi \times (\mathrm{DBH} / 2)^2$, and any equation here using BA can be reformulated using DBH. There was a linear relationship between BA and coarse root dry mass (Norby et al., 2001):

$$M_{root} = 0.049 \times A_{1.3} + 4.91; \; n = 10, r^2 = 0.85 \quad (2)$$

Circumference at 1.3 m height of each tree within the plots was measured monthly from which BA was calculated. H and T were measured annually on a subset of trees, and from these measurements, average AGB and annual plot-level dry mass increment (kg m^{-2}) were calculated and used in assessment of NPP (Norby et al., 2010).

In July 2009, in the 12th year of CO_2 treatment, we harvested 16 dominant or co-dominant trees (Figure 1). We chose four trees from each of the two eCO_2 plots and eight trees total from the three aCO_2 plots. These trees were at the periphery of the plots so that they could be felled to a cleared area outside the plot to avoid damage to the crown, the residual trees in each plot, and the FACE infrastructure (eCO_2 treatment in the plots continued until October 2009.) Six of the trees in eCO_2 plots had been measured throughout the experiment; the other two were in the buffer zone and so had been exposed to eCO_2 but not measured during the experiment. Five of the eight aCO_2 trees had been routinely measured. The height and BA of the 16 trees covered 60%–67% of the full range of the 409 trees in the experimental plots, and importantly (for useful allometry), only 8% of the trees in the plots were taller or had greater BA. Processing of each tree began immediately after it was felled. Bole length and circumference at 1.3 and 4 m height were measured, and 1 m height increments were marked on the bole with lumber crayon. Leaves were removed by 1 m height increment, weighed, and subsampled as described by Norby et al. (2022). When leaf removal was complete, sections of the bole of approximately 0.5 m (lower bole) to 2 m (upper bole) length were cut with a chain saw and weighed on a veterinary balance (0.1 kg resolution) (Figure 1). Some of these sections were frozen for use in subsequent studies of wood anatomy and chemistry (Eberhardt et al., 2015; Kim et al., 2015). Four disks of approximately 5 cm thickness distributed across the entire bole (0.5, 1.3, 4, 8, and 12 m or base of crown) were cut and weighed on a large-capacity analytical balance (0.1 g resolution). These disks were oven-dried at 70°C until constant weight was achieved, generally requiring several days, for determination of dry-to-fresh mass ratio. Additional disks

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FIGURE 1 Felling, bucking, and weighing of *Liquidambar syraciflua* tree boles from the Oak Ridge National Laboratory (ORNL) free-air CO_2 enrichment experiment in July 2009 and root extraction and cleaning in November 2009. *Source*: All photos by R. J. Norby, ORNL. Videos of the felling, bucking, and weighing are available here: http://tinyurl.com/3e9atvxe; http://tinyurl.com/de334k26; and http://tinyurl.com/bdfbmhka.

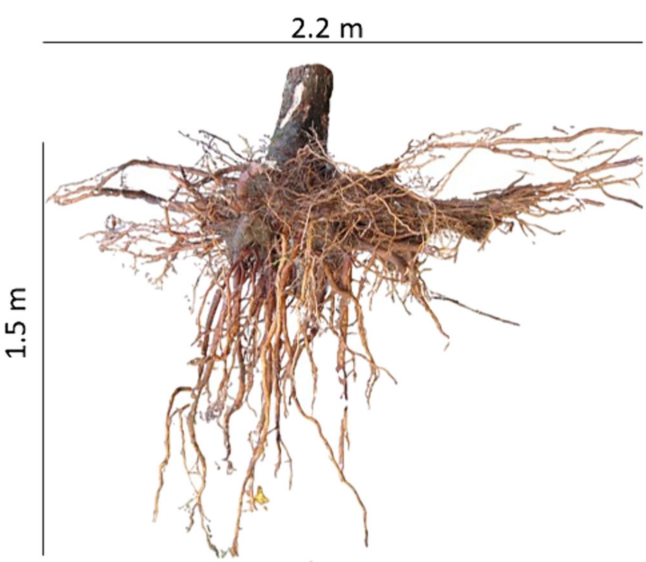

FIGURE 2 Typical root system of a *Liquidambar syraciflua* tree extracted from the Oak Ridge National Laboratory free-air CO_2 enrichment experiment, showing the spread of lateral roots in the upper 25 cm of soil and vertically oriented roots extending deeper in the soil. The horizontal and vertical scales are approximate.

of 2–3 cm thickness were cut, weighed on the analytical balance, and frozen for use in ancillary studies. Branches were weighed fresh, and subsamples weighed, oven-dried, and weighed again.

The coarse woody root system of 10 trees was extracted from the ground, washed, and quantified in November 2009 (Figure 1). The choice of trees was limited by the need for access by the heavy equipment used to extract them. Five trees were from an eCO_2 plot, including three that had been previously felled and processed in July. Five additional trees were from an area of the plantation outside of an experimental plot, but nevertheless considered in aCO_2. Those trees that had not previously been measured for AGB were sampled and measured as described above, except since they were leafless in November, leaf removal was not included. To remove the stump and attached lateral roots, a front-end loader pushed the high stump back and forth to loosen it and then lifted the intact root system from the soil (Figure 1). This approach resulted in a nearly complete volumetric recovery of the woody root system. A few lateral roots that had been sheared off and remained in the soil were extracted with shovels; these roots comprised a very small fraction of the total dry mass. The intact root system was washed free of most soil with a high-pressure hose. Further cleaning was done with a low-pressure hose. Lateral

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TABLE 1 Data from harvests of *Liquidambar styraciflua* trees in a free-air CO_2 enrichment (FACE) experiment at the Oak Ridge National Laboratory.

Ring #	Tree #	Harvest date	CO_2	DBH, cm	$A_{1.3}$, cm^2	A_4, cm^2	H, m	Bole mass, kg	Branch mass, kg	AGB, kg	Predicted AGB, kg
1	1	Aug 1996	Pre-treat	10.4	85.3	52.8	12.40			19.98	27.03
1	2	Aug 1996	Pre-treat	9.9	76.4	41.6	12.00			25.07	20.34
1	3	Aug 1996	Pre-treat	6.5	33.3	18.1	10.20			9.48	10.28
2	1	Aug 1996	Pre-treat	15.2	180.6	113.2	13.60			57.29	51.79
2	2	Aug 1996	Pre-treat	13.0	133.2	88.5	13.20			39.59	41.77
2	3	Aug 1996	Pre-treat	10.8	91.5	58.5	11.90			32.00	28.69
5	5	Aug 1996	Pre-treat	12.0	113.1	75.2	13.70			38.26	38.15
5	6	Aug 1996	Pre-treat	10.0	79.3	55.4	12.10			26.58	29.79
0	1	July 1999	Ambient	15.1	178.0	99.7	14.94			44.01	51.52
0	2	July 1999	Ambient	15.5	188.7	131.2	15.91			64.34	65.15
0	3	July 1999	Ambient	14.0	154.3	122.3	16.14			67.21	61.80
0	4	July 1999	Ambient	15.6	192.3	141.0	16.07			66.28	68.86
0	5	July 1999	Ambient	14.6	167.0	106.6	14.29			52.34	51.22
0	6	July 1999	Ambient	19.0	284.3	215.2	16.67			97.13	98.84
0	7	July 1999	Ambient	12.7	127.5	93.1	15.75			50.91	49.86
0	8	July 1999	Ambient	14.0	153.7	90.9	16.29			54.10	50.59
0	9	July 1999	Ambient	10.1	80.7	63.3	13.71			35.49	37.29
0	10	July 1999	Ambient	13.5	142.8	100.3	15.86			50.74	52.75
1	78	July 2009	Elevated	11.6	106.4	76.0	17.35	26.84	4.72	31.56	46.13
1	79	July 2009	Elevated	15.0	176.0	115.5	18.15	61.6	1.8	63.39	66.31
1	86	July 2009	Elevated	20.7	338.1	243.4	19.50	111.2	23.6	134.82	129.04
1	186	July 2009	Elevated	17.0	227.5	140.4	18.65	59.1	13.9	73.00	82.32
2	4	July 2009	Elevated	20.8	339.6	264.0	21.30	117.08	14.53	131.61	143.46
2	10	July 2009	Elevated	20.0	313.7	211.1	21.50	102.74	9.13	111.87	129.03
2	11	July 2009	Elevated	22.0	381.8	211.1	20.15	120.68	18.77	139.45	138.72
2	204	July 2009	Elevated	20.4	326.0	240.7	21.27	137.52	14.93	152.45	136.05
3	3	July 2009	Ambient	19.1	285.6	207.0	21.86	105.97	6.91	112.88	123.24
3	4	July 2009	Ambient	15.8	195.8	141.0	19.25	73.47	4.18	77.65	79.95
3	303	July 2009	Ambient	18.5	269.6	179.5	21.90	104.72	4.69	109.41	114.02
4	2	July 2009	Ambient	14.1	157.0	128.6	18.68	55.42	4.17	59.59	71.00
4	404	July 2009	Ambient	18.4	264.8	187.2	19.57	97.49	12.18	109.67	103.77
5	20	July 2009	Ambient	20.0	315.4	236.4	21.42	141.82	15.08	156.90	133.57
5	521	July 2009	Ambient	17.5	241.1	131.1	21.02	50.61	5.88	56.49	99.60
5	522	July 2009	Ambient	19.9	310.1	212.7	21.33	103.40	11.29	114.69	127.51
0	1	Nov 2009	Ambient	19.2	288.5	127.4	21.25	95.89	3.89	99.78	105.88
0	2	Nov 2009	Ambient	18.2	260.9	164.7	19.90	81.37	4.57	85.94	100.50
0	3	Nov 2009	Ambient	11.8	109.0	84.6	15.70	34.27	0.96	35.23	46.39
0	4	Nov 2009	Ambient	21.7	370.4	255.8	21.53	134.98	7.66	142.64	152.90
0	5	Nov 2009	Ambient	16.4	210.7	153.4	20.71	68.98	3.11	72.09	91.31
2	5	Nov 2009	Elevated	14.6	167.2	105.4	17.76	56.05	2.49	58.54	70.65
2	9	Nov 2009	Elevated	12.7	127.3	73.1	14.30	35.84	1.58	37.42	37.72

Note: Trees were harvested at the beginning of the experiment (1996 and 1999) and at the end (2009). FACE rings 1 and 2 were in elevated CO_2, rings 3, 4, and 5 were ambient CO_2 FACE rings, and ring 0 designates areas between FACE rings (ambient CO_2). DBH is tree diameter at 1.3 m height; H is total tree height; $A_{1.3}$ and A_4 are cross-sectional areas at 1.3 m height (basal area, BA) and 4 m height. Predicted aboveground biomass (AGB, bole + branch) is based on the initial allometric equation (Equation 1). Data from 1996 and 1999 harvests are from Norby et al. (2001); AGB was not separated into bole and branch in those harvests. The trees were 9 years old in 1996, 12 years old in 1999, and 22 years old in 2009.

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TABLE 2 Dry mass of coarse woody root systems of *Liquidambar styraciflua* trees excavated from the Oak Ridge National Laboratory free-air CO_2 enrichment (FACE) experiment in 1999 and 2009.

Ring #	Tree #	Harvest date	CO_2	Root mass, kg	Root fraction, %	Predicted root mass, kg
0	1	July 1999	Ambient	14.05	24.2	13.63
0	2	July 1999	Ambient	14.35	18.2	14.15
0	3	July 1999	Ambient	14.21	17.4	12.47
0	4	July 1999	Ambient	13.77	17.2	14.33
0	5	July 1999	Ambient	11.23	17.7	13.09
0	6	July 1999	Ambient	19.39	16.6	18.84
0	7	July 1999	Ambient	10.48	17.1	11.16
0	8	July 1999	Ambient	12.77	19.1	12.44
0	9	July 1999	Ambient	9.90	21.8	8.86
0	10	July 1999	Ambient	10.73	17.5	11.91
2	4	Nov 2009[a]	Elevated	48.46	26.9	21.54
2	5	Nov 2009	Elevated	12.55	17.7	13.10
2	9	Nov 2009	Elevated	10.66	22.2	11.15
2	10	Nov 2009[a]	Elevated	24.88	18.2	20.28
2	11	Nov 2009[a]	Elevated	32.59	18.9	23.61
0	1	Nov 2009	Ambient	26.87	21.2	19.04
0	2	Nov 2009	Ambient	24.11	21.9	17.69
0	3	Nov 2009	Ambient	8.65	19.7	10.25
0	4	Nov 2009	Ambient	38.01	21.0	23.05
0	5	Nov 2009	Ambient	18.97	20.8	15.23

Note: Ring 0 refers to areas of the plantation outside of FACE rings. Root fraction is coarse root mass divided by total tree wood mass. Predicted coarse root mass is based on the initial allometric equation (Equation 2).
[a]Aboveground portion of tree was harvested and processed in July 2009.

and vertical spread of residual coarse roots was measured (Figure 2). Lateral roots and the belowground portion of the stump were oven-dried and weighed, and the aboveground portion of the stump was subsampled with a disk and processed as with the rest of the bole. Fine roots (i.e., <2 mm diameter) were not recovered in the coarse root processing but were assessed separately as previously described (Iversen et al., 2012). Fine-root mass per tree was approximately 0.7 kg, less than 3% of total root mass, based on quantification of fine-root mass per unit soil volume determined in deep pits dug in the FACE plots in 2009 (Iversen et al., 2012) and the approximate soil volume occupied by the coarse root system.

The dry-to-fresh mass ratio of the subsampled disks from the bole was calculated, and fresh mass of all other bole sections was calculated using the ratio of the nearest disk. Total AGB is the sum of all bole sections, the aboveground stump, and branches. Total belowground dry mass is the sum of belowground stump plus lateral roots.

H, T, and BA of the harvested trees were used to predict AGB using Equation (1) in the same way as done throughout the experiment. Coarse root mass was calculated using Equation (2). The predicted masses were compared to measured AGB and coarse root mass, and the percentage differences between predicted and measured were calculated. Measured AGB was regressed against predicted values to test if significant prediction errors were present (Sileshi, 2014). New allometric relationships were developed between DBH or BA and AGB and coarse root mass using all harvested trees from 1996, 1999, and 2009 using Stata SE/18.0 software.

3 | RESULTS

The trees harvested in 2009 ranged in height from 14.3 to 21.9 m and in BA from 106 to 382 cm^2 (DBH from 11.6 to 22.0 cm) (Table 1). The bole comprised 92% of AGB, and coarse root biomass comprised 21% of total tree wood mass (Table 2). AGB of trees grown in aCO_2 was 97 ± 9 and 93 ± 14 kg in eCO_2, but we caution that the harvested trees did not represent a random sample from the experimental plots, were not from the interior of the FACE plots, and about half of this mass (46 ± 5 kg) was present at the beginning of the experiment. Dry mass of the bole at 1.3 m height was 50 ± 2% of wet mass when trees were felled and did not vary by treatment. Extracted root systems varied, but most were dimorphic with many coarse lateral and fine roots occupying the surface layers, and a distinct pattern of coarse roots extending vertically down (Figure 2). The downward extending roots were narrower-diameter coarse roots that likely contributed a small amount to the overall coarse root mass. Coarse root mass was 23 ± 5 kg in aCO_2, 26 ± 7 kg in eCO_2, and 13 ± 1 kg at the beginning of the experiment. Coarse root depth of extracted stumps ranged from 1.1 to 2.2 m as previously reported by Warren et al. (2011), with

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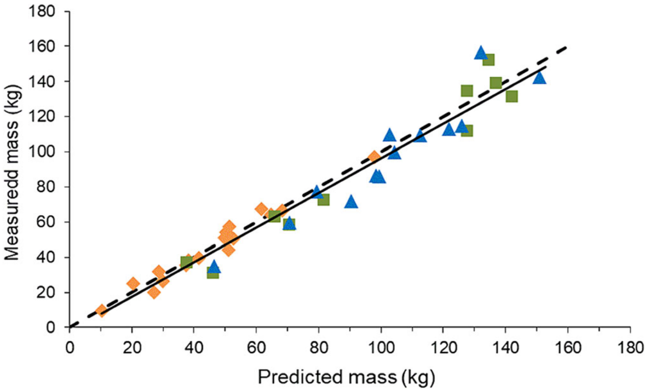

FIGURE 3 Regression of measured aboveground biomass of harvested *Liquidambar syraciflua* trees against predicted values. Orange symbols are trees harvested from the Oak Ridge National Laboratory free-air CO_2 enrichment experiment in 1996 and 1999 from which the prediction equation (Equation 1) was established. Blue symbols are trees from final harvest in 2009 in aCO_2, and green symbols are trees in eCO_2. The solid line is the regression, and the dashed line shows the 1:1 relationship. The slope of the regression (0.98) is not significantly different from 1, and the intercept (−2.14) is not significantly different from 0.

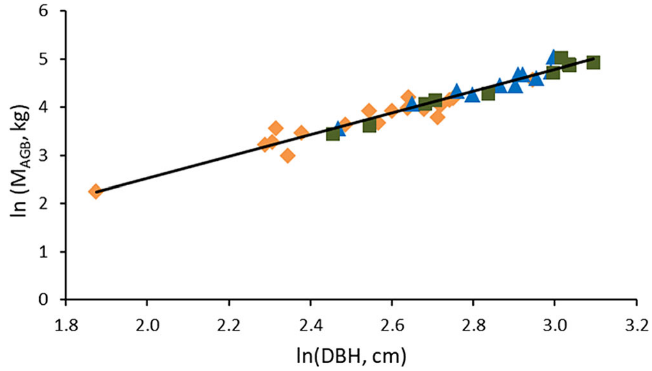

FIGURE 4 Allometric equation between bole diameter at 1.3 m (diameter at breast height [DBH]) and aboveground biomass (M_{AGB}) established on all *Liquidambar syraciflua* trees harvested from the Oak Ridge National Laboratory free-air CO_2 enrichment experiment in 1996 and 1999 (orange symbols) and in 2009 from aCO_2 (blue symbols) and eCO_2 (green symbols). Regression equation is $\ln(M_{AGB}) = -1.997 + 2.263 \times \ln(DBH)$; $n = 41$, $r^2 = 0.95$.

a similar lateral coarse root spread, although some terminal roots were broken and not located, indicating deeper maximum rooting (Figure 2).

Ten of the 23 trees harvested in 2009 were larger than the largest trees used to establish the aboveground allometry in 1996 and 1999. Also, 10 of the harvested trees grew in eCO_2, unlike any of the calibration trees. Either of these factors might have invalidated the allometry used throughout the 12 year experiment. However, there was little deviation in AGB of the harvested trees from the prediction by the allometric equation (Figure 3). The regression indicates no significant prediction errors (Sileshi, 2014). Average AGB of the harvested trees was overestimated by the allometry by 6.4% across all trees. Trees harvested in 2009 were underestimated by 10.0% in aCO_2 and 9.4% in eCO_2.

Combining the data from trees harvested in 1997, 1999, and 2009, a new and simpler allometry can be established, based only on DBH (Figure 4). This new allometry (Equation 3, Table 3) predicts the measured AGB within 0.13% across all trees. Trees harvested in 2009 were underestimated by 1.9% in aCO_2 and overestimated by 3.2% in eCO_2.

$$M_{AGB} = \exp\left(-1.997 + 2.263 \times \ln(DBH); n = 41, r^2 = 0.95. \quad (3)$$

The initial allometric equation for coarse root mass was a linear function with BA. With the 2009 harvested root systems included, the data were best described by an exponential relationship (Equation 4; Figure 5, Table 3).

$$M_{root} = 5.532 \times \exp(0.00519 \times BA); n = 20, r^2 = 0.82 \quad (4)$$

Coarse root mass of the 2009 trees was underestimated by the original allometry by 28.8%, with the largest discrepancies occurring in the largest trees (Table 2). An exponential fit to the initial data set, which would have been difficult to justify based on the data at hand, would still have underestimated the final harvested root mass. Root mass represented 20.9% of total wood mass (Table 1), consistent with root fraction of hardwood forests in the United States (Cairns et al., 1997). The deviations in estimates of aboveground and root mass from direct measurements were offsetting, so the predictions of total wood mass based on the two initial allometric equations used throughout the experiment were only 1.9% greater than the measured mass (2.7% greater than final harvested trees).

4 | DISCUSSION

The allometric equations developed at the beginning of the ORNL FACE experiment (Norby et al., 2001) proved to be reliable predictors of tree growth for the duration of the experiment. Although the linear equation for coarse root mass versus BA underestimated final root mass, the error for total tree mass was small. Our hypothesis is supported by the results presented here, and the alternative hypothesis is rejected: The calculations derived from the allometry used throughout the experiment do not require revision. Generally, simple allometric equations are preferred over ones with multiple parameters (Sileshi, 2014), although inclusion of T can improve estimates (Temesgen et al., 2015). We had good reason to include additional terms in the AGB allometry (Hand T) given the evidence that allometry can change with ontogeny or environmental influences (e.g., elevated CO_2) (McCarthy et al., 2010). However, there was no evidence that the allometry changed during the course of the experiment, and with hindsight, a regression based simply on DBH would

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TABLE 3 Allometric equations for aboveground biomass (AGB) and coarse root mass of *Liquidambar styraciflua* trees.

Dependent variable	Equation	*n*	β_0	β_0 [se]	β_1	β_1 [se]	r^2	RMSE %
M_{AGB}	$\exp(\beta_0 + \beta_1 \times \ln(DBH))$	41	−1.997	0.217	2.263	0.080	0.95	13.4
M_{root}	$\beta_0 \times \exp(\beta_1 \times BA)$	20	5.7846	1.027	0.00511	0.00058	0.82	23.3

Note: M_{AGB} and M_{root} are dry mass of aboveground biomass and coarse root (kg); DBH is tree diameter at breast height (cm); BA is cross-sectional area (cm^2); β_0 and β_1 are coefficients in the allometric equation; se is standard error; RMSE % is root mean square error as a percent of absolute value.

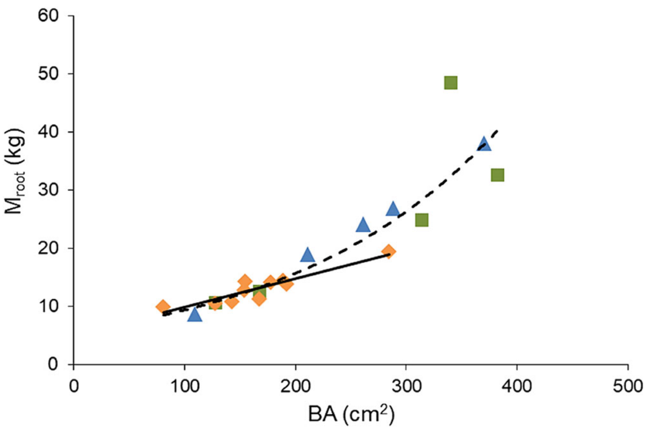

FIGURE 5 Comparison of initial coarse root mass allometry and allometry established after final harvest of *Liquidambar syraciflua* trees from the Oak Ridge National Laboratory free-air CO_2 enrichment experiment. Orange symbols are coarse root systems harvested in 1999 from which the linear allometric equation predicting root dry mass (M_{root}) from tree basal area (BA) was established (solid line, Equation 2). Dotted line is regression established with both the 1999 trees and root systems harvested in 2009 from aCO_2 (blue symbols) and eCO_2 (green symbols): $M_{root} = 5.746 \times \exp(0.00511 \times BA)$; $n = 20$, $r^2 = 0.82$.

have been more robust, especially given the difficulty in measuring T and Hof the standing trees. However, we would not have had full confidence in our estimates of tree growth and NPP without accounting for possible changes in tree morphology during the experiment. We were fortunate to be able to harvest trees at our site to establish site-specific relationships, but harvesting trees during the experiment was precluded.

Expensive, long-term forest experiments cannot wait for a final harvest to deliver results, and we must accept the inevitable uncertainty in estimates of tree dry matter increment that the reliance on allometry entails. The problem is more acute for the current generation of FACE experiments (Norby et al., 2016) being conducted in mature stands with much larger trees, where destructive harvests are precluded. TLS now offers a non-destructive approach to measuring tree volume and, when combined with wood density, AGB (Calders et al., 2015). TLS is considered a robust and more precise estimate of AGB than traditional allometry and can effectively replace the need for destructive sampling (Stovall et al., 2023). Had TLS been available in 1996 at the start of the ORNL FACE experiment (TLS was introduced for forest measurements in the early 2000s; Calders et al., 2020), allometry could have been based on TLS determination of AGB of each tree in the plots rather than of a small subset of 18 trees. Additional TLS scans during the experiment would have provided checks on whether a revision in the allometric equations was needed. Quantification of coarse root biomass still requires a destructive harvest, although improvements in three-dimensional ground penetrating radar for estimation of coarse root volume (Rocha et al., 2024) may provide a useful non-destructive approach. Assuming a constant ratio with AGB can be an acceptable and necessary compromise.

At the AmazonFACE experiment in a tropical forest, almost every tree is a different species. Calculation of tree volumes with TLS, combined with species-specific wood density values, should be more reliable than application of generic allometry for tropical trees (Chave et al., 2005; Momo Takoudjou et al., 2018). The value of TLS determination of AGB in an ongoing FACE experiment was apparent in the Birmingham Institute of Forest Research (BIFoR) FACE experiment in central England (Hart et al., 2020). The experiment is of similar design to the ORNL FACE experiment, except the *Quercus robur* trees are 180 years old and 100-fold larger than the *Liquidambar* trees at ORNL FACE. Harvesting trees at the site for determination of allometric equations was precluded for reasons of site conservation and at any rate would have been an extremely difficult and expensive task. Hence, AGB estimates were originally based on a published equation for the species (Forrester et al., 2017), which was primarily developed from a harvest of trees in northwestern Spain. The applicability of this equation was in doubt, however, because 49% of the trees at BIFoR FACE are larger than the largest tree in the data base used to establish the regression equation (Norby et al., 2024). Once a TLS scan of the BIFoR FACE site was completed (Klaske van Wijngaarden, personal communication), a more reliable, site-specific basis for an allometric equation was established and used to quantify AGB and its response to eCO_2 (Norby et al., 2024). The TLS-based allometry reduced estimates of dry matter increment by 17%, with follow-on effects on quantification of NPP and allocation.

Uncertainty in tree biomass estimation cannot be avoided. Transparent assessment of the allometry employed in these estimates of tree biomass is essential for scientific and public confidence in policy initiatives that are informed by those estimates. TLS has revolutionized the monitoring and quantification of forest structure and function and is being used in a range of ecological applications (Calders et al., 2020). An especially high priority is reducing uncertainty in regional and national forest carbon estimates needed for evaluation of forests as natural climate solutions (Calders et al., 2022). The response of tree biomass in FACE and other global change experiments is another critical element in evaluations of the climate change implications of carbon cycle feedbacks between the terrestrial biosphere and

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the atmosphere as the atmospheric concentration of CO_2 increases (Medlyn et al., 2015). Hence, the new generation of FACE experiments should employ TLS to reduce the uncertainty in estimates of tree growth responses to elevated CO_2.

AUTHOR CONTRIBUTIONS

Richard J. Norby wrote the paper with input from Jeffrey M. Warren, Colleen M. Iversen, and Anthony P. Walker. Richard J. Norby, Jeffrey M. Warren, Colleen M. Iversen, Anthony P. Walker, and Joanne Childs participated in the tree harvest.

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CONFLICT OF INTEREST STATEMENT

None declared.

DATA AVAILABILITY STATEMENT

The data used in this paper are presented in Tables 1 and 2.

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