Received: 19 August 2021 | Accepted: 15 October 2021

DOI: 10.1111/gcb.15999

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

The response of coarse root biomass to long-term CO_2 enrichment and nitrogen application in a maturing *Pinus taeda* stand with a large broadleaved component

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Funding information
US Forest Service , Southern Research Station; US Department of Energy, Grant/Award Number: DE-SC0006967 and DE-AC05-00OR22725

Abstract

Elevated atmospheric CO_2 (eCO_2) typically increases aboveground growth in both growth chamber and free-air carbon enrichment (FACE) studies. Here we report on the impacts of eCO_2 and nitrogen amendment on coarse root biomass and net primary productivity (NPP) at the Duke FACE study, where half of the eight plots in a 30-year-old loblolly pine (*Pinus taeda*, L.) plantation, including competing naturally regenerated broadleaved species, were subjected to eCO_2 (ambient, aCO_2 plus 200 ppm) for 15–17 years, combined with annual nitrogen amendments (11.2 g N m^{-2}) for 6 years. Allometric equations were developed following harvest to estimate coarse root (>2 mm diameter) biomass. Pine root biomass under eCO_2 increased 32%, 1.80 kg m^{-2} above the 5.66 kg m^{-2} observed in aCO_2, largely accumulating in the top 30 cm of soil. In contrast, eCO_2 increased broadleaved root biomass more than twofold (aCO_2: 0.81, eCO_2: 2.07 kg m^{-2}), primarily accumulating in the 30–60 cm soil depth. Combined, pine and broadleaved root biomass increased 3.08 kg m^{-2} over aCO_2 of 6.46 kg m^{-2}, a 48% increase. Elevated CO_2 did not increase pine root:shoot ratio (average 0.24) but increased the ratio from 0.57 to 1.12 in broadleaved species. Averaged over the study (1997–2010), eCO_2 increased pine, broadleaved and total coarse root NPP by 49%, 373% and 86% respectively. Nitrogen amendment had smaller effects on any component, singly or interacting with eCO_2. A sustained increase in root NPP under eCO_2 over the study period indicates that soil nutrients were sufficient to maintain root growth response to eCO_2. These responses must be considered in computing coarse root carbon sequestration of the extensive southern pine and similar forests, and in modelling the responses of coarse root biomass of pine–broadleaved forests to CO_2 concentration over a range of soil N availability.

KEYWORDS
allometry, biomass, carbon, coarse root, elevated CO_2, free-air CO_2 enrichment, net primary production, *Pinus taeda* (loblolly pine)

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1 | INTRODUCTION

The long-term trajectory of forest net primary productivity (NPP) under increasing atmospheric [CO_2] is variable, ranging from strongly positive to no response (Nowak et al., 2004). How forests respond to elevated CO_2 (eCO_2) depends to a large degree on resource limitations of NPP under ambient CO_2 (aCO_2) (e.g. light, water, nutrients) (Kim et al., 2016; Körner, 2003a, 2003b; Oren et al., 2001). The stimulation of growth from eCO_2 may not occur in ecosystems that are strongly coupled to native nutrient cycling (e.g. *steady-state nutrient cycle—Type III response*, Körner, 2006). For example, in an early succession pine stand on nutrient-poor sandy soil, a growth response to eCO_2 was only observed with addition of supplemental nutrients (Oren et al., 2001). Similarly, experiments in late succession spruce (Sigurdsson et al., 2013) and eucalyptus (Ellsworth et al., 2017) forests where growth at aCO_2 was limited by nutrient availability, no growth response to eCO_2 were observed. In both studies, eCO_2 induced a growth response after nutrient limitations were alleviated (i.e. by fertilization). The stimulation of tree growth by eCO_2 may be ephemeral if nutrients become progressively scare, being tied up in organic matter (Luo et al., 2004; Norby et al., 2010). In two free-air carbon enrichment (FACE) studies in a pine and broadleaved plantations (Norby et al., 2010; Oren et al., 2001), early increases in tree stem growth from a step increase in [CO_2] were not sustained due to decreasing soil nutrients or nitrogen availability.

Forests allocate 20%–65% of NPP belowground to support growth and maintenance of roots and mycorrhizae (Landsberg & Sands, 2011), thus a complete accounting of biomass partitioning, particularly belowground, is necessary to understand and predict forest response to eCO_2 (Walker et al., 2019). Long-term eCO_2 experiments performed at the tree and stand scale generally show that CO_2 enrichment increases belowground carbon allocation (Finzi et al., 2007; Iversen et al., 2012; Matamala & Schlesinger, 2000; Norby et al., 2004; Pritchard et al., 2008a, 2008b) and the magnitude of the response is inversely correlated with aboveground sink strength, which increases with soil fertility (Palmroth et al., 2006). Ecological studies of forest root systems generally distinguish a fine and coarse root fraction based on root diameter as each have different morphological and functional traits, decomposition dynamics and response to resource availability (Litton et al., 2007; Poorter & Nagel, 2000). Fine roots (<2 mm diameter) are important for resource acquisition, have high nutrient concentration and are relatively short-lived, whereas, larger coarse roots (>2 mm diameter) are perennial, support fine root networks, transport water and nutrients, store carbohydrates and provide physical support for aboveground biomass (AGM; Landsberg & Sands, 2011). Both root fractions will likely play a key role in the ability of forests to sequester carbon (Johnsen et al., 2001; Norby & Jackson, 2000). Fine root production represents a large fraction of annual NPP and provides a large input of soil carbon and nitrogen through rapid root turnover (Ainsworth & Long, 2005; Bonan, 2008). Quantifying the turnover rate of this pool is, however, subject to large uncertainties (Strand et al., 2008). In contrast, coarse roots, which account for up to 80% of belowground biomass (Butnor et al., 2003) and 10%–20% of NPP (Giardina & Ryan, 2002; Maier et al., 2004), contribute to ecosystem carbon storage through formation of long-lived live wood biomass (Mobley et al., 2013) that can persist for decades following senescence (e.g. after forest harvest) (Anderson et al., 2018; Clark et al., 2001; Johnsen et al., 2001; Ludovici et al., 2002). Indeed, ecosystem retention of carbon over the long term may be determined by the fraction allocated to perennial woody biomass with slow turnover and mean residence time of decades or longer (Walker et al., 2019).

Results from large-scale field experiments in conifers and broadleaved species generally show that long-term CO_2 enrichment stimulates fine root production and increases biomass (Matamala & Schlesinger, 2000; Norby et al., 2004; Phillips et al., 2006; Pritchard et al., 2008a), root length and rooting depth (Taylor et al., 2014). Interestingly, eCO_2 increased fine root turnover in pine (Pritchard et al., 2008a), but decreased turnover in broadleaved *Liquidambar styraciflua* (Iversen et al., 2008). Compared to the wealth of data for fine roots, less effort has been made to study how eCO_2 affects coarse roots. While it is expected that CO_2 enrichment will stimulate coarse root biomass, less is known about how eCO_2 affects above- and belowground biomass partitioning and coarse root structure. This is in part because measuring the effects of eCO_2 on coarse root biomass of trees is difficult owing to the size and scale of the experimental unit and duration of eCO_2 exposure necessary to obtain meaningful results. Allometric biomass partitioning theory suggests that there is a stable isometric relationship between coarse root and stem biomass or root:shoot ratio (R/S) (Niklas & Spatze, 2006) and that coarse root biomass will change in unison with AGM (McCarthy & Enquist, 2007). Species-specific R/S is widely used for estimating coarse root biomass in forest ecosystems (Mokany et al., 2006) and developing forest carbon budgets (Cairns et al., 1997; Li et al., 2003; Snowdon et al., 2003), thus a stable relationship between coarse root and shoot biomass would simplify modelling forest response to eCO_2. Nevertheless, evidence for eCO_2 effects on R/S is equivocal. Field experiments using open-top chambers and FACE found no effect of eCO_2 on R/S in some conifers (Crookshanks et al., 1998; Tissue et al., 1997) and broadleaved species (Calfapietra et al., 2003; Gielen et al., 2005; Norby et al., 1995). In contrast, Day et al. (2013) found for a scrub-oak ecosystem that long-term eCO_2 increased above and belowground biomass, but the absolute increase was greater for root biomass meaning that R/S increased under eCO_2.

1.1 | Duke free-air carbon enrichment study

The long-term effects of eCO_2 on forest structure and function were studied in a *P. taeda* forest at the Duke FACE experiment from 1994 to 2010. Exposure to eCO_2 resulted in a sustained increase in photosynthesis in pine (Maier et al., 2008) and broadleaved (Ellsworth et al., 2012) species. Early in the study, 41% greater annual canopy photosynthesis (Schäfer et al., 2003) under eCO_2 resulted in a 13%–27% increase in tree basal area growth (Moore et al., 2006), a 27% increase in annual wood increment (Hamilton et al., 2002) and a

21% increase in stand NPP (McCarthy et al., 2010). Plot variability in soil nitrogen availability explained much of the variation in NPP, as there was a linear response of NPP to a plot-level index of soil nitrogen availability (Finzi et al., 2002; McCarthy et al., 2010). Kim et al. (2020) further showed that long-term eCO_2 altered the aboveground allometric relationship for pine, specifically an increase in height/diameter ratio. Accounting for shifts in allometry increased the effects of eCO_2 on aboveground pine biomass from 21% to 27%. They found no eCO_2 response in aboveground allometry of broadleaved species.

Increased belowground carbon allocation under eCO_2 supported greater nitrogen uptake and sustained aboveground production due to a combination of increased fine root production, soil organic matter decomposition, and carbon allocation to mycorrhizal fungi (Drake et al., 2011; Finzi et al., 2007), increased fine root respiration (Drake et al., 2008) and soil CO_2 efflux (Butnor et al., 2003; Kim et al., 2017; Palmroth et al., 2006). Pritchard et al. (2008a, 2008b), using minirhizotrons, found that fine root biomass distribution and mycorrhizal fungi increased at deeper depths, and Taylor et al. (2014), using soil monoliths, found that CO_2 enrichment increased fine root length and shifted fine root distribution to smaller size classes (<1 mm). There are limited data from the Duke FACE study on the direct effects of eCO_2 on coarse root biomass. Early stand-level estimates of coarse root biomass relied on allometric equations developed prior to CO_2 treatment (Finzi et al., 2006; Hamilton et al., 2002; Naidu et al., 1998; Schäfer et al., 2003) or estimated coarse root biomass as a function of AGM (McCarthy et al., 2010) assuming no CO_2 induced shifts in R/S. An exception was Jackson et al. (2009). They measured coarse root biomass (pine + broadleaved) in 5 cm diameter by 15 cm deep soil cores. Periodic measurements from 2003 to 2009 showed that eCO_2 treatments had on average 17% more coarse root biomass, but this difference was not significant. However, a one-time sampling in 2008 from larger 0.13 m^3 pits found a significant doubling of coarse root biomass in eCO_2 treatments, much higher than the 21% increase in aboveground biomass over the same period (McCarthy et al., 2010).

In this study, we evaluated how up to 17 years of CO_2 enrichment and 6 years of annual nitrogen amendments at the Duke FACE site affected standing coarse root biomass and NPP for dominant pine (*P. taeda*) and broadleaved competitors. We developed allometric equations to predict coarse root biomass for the pine (taproot and lateral roots >2 mm in diameter) and broadleaved species and explore the effects of eCO_2 with and without nitrogen amendment on stand coarse root biomass, vertical distribution with respect to root diameter class, R/S and how eCO_2 and supplemental nitrogen affected NPP. We hypothesized that eCO_2 would increase coarse root biomass for canopy pine and broadleaved trees present both in the pine-dominated layer and below (**H1a**), that increased biomass under eCO_2 would shift coarse root biomass distribution with depth (**H1b**), and that smaller diameter roots would be more responsive to eCO_2 than larger diameter roots (**H1c**). We further hypothesized that the amount of increased coarse root biomass would be greater than that observed for aboveground components (i.e. increased R/S) (**H2**). Because the magnitude of aboveground growth response to eCO_2 was constrained by nutrient availability (McCarthy et al., 2010; Oren et al., 2001), we hypothesized nitrogen additions would increase coarse root biomass mostly in the eCO_2 treatment (i.e. a CO_2 × nitrogen interaction) (**H3**). Our results provide a more complete assessment of the long-term effects of eCO_2 on stand development as reflected in carbon production and partitioning in coarse root biomass.

2 | MATERIALS AND METHODS

2.1 | Site description

The Duke FACE experiment was located in a 90-ha loblolly pine (*Pinus taeda*, L.) plantation in the Blackwood Division of the Duke Forest (Orange County, NC; 35°97′N, 79°09′W). Three-year-old half-sib seedlings were planted in 1983 at 2.0 × 2.4 m spacing following a chop and burn site preparation treatment. The climate is warm, humid in the summer and moderate in the winter with a mean annual temperature of 15.5°C. Mean annual precipitation is 1145 mm and is evenly distributed throughout the year. The soils are predominantly Enon silt-loam characterized as a moderately low fertility acidic clay loam. Soil pH is around 6.0, and pine foliage N (~1.1%) and phosphorus (~0.3%) tend to be at the middle range for mid-rotation *P. taeda*. The site index is 21 m at age 25. Loblolly pine comprised 89% of basal area in 2010. Other common woody plants include sweetgum (*Liquidambar styraciflua*) in the mid- to upper forest canopy, and winged elm (*Ulmus alata*), dogwood (*Cornus florida*) and red maple (*Acer rubrum*) in the mid- to lower canopy.

The FACE experiment consisted of eight circular plots measuring 30 m in diameter. A prototype (FACEp) plot with elevated CO_2 (eCO_2) and a reference plot with ambient CO_2 (aCO_2) were established in 1993 when the trees were 13 years old. The replicated FACE experiment established six additional plots (three each of eCO_2 and aCO_2) in 1996. The eCO_2 plots received additional CO_2 to maintain atmospheric [CO_2] at ambient +200 μl L^{-1}, while the aCO_2 plots received only ambient air. Carbon dioxide enrichment commenced in 1994 and 1996, for the FACEp and FACE experiments, respectively, and continued through October 2010. Details on FACE operation and protocols for quality control and assurance are in Hendrey et al. (1999).

From 1998 to 2004, the FACEp plots received a nutrient addition treatment. Each plot was split in half by an impermeable barrier down to 70 cm, below most of the fine roots (Matamala & Schlesinger, 2000), and one half of each plot was fertilized annually with 5.6 or 11.2 g N m^{-2} as NH_4NO_3 or urea (N) and balanced with other nutrients as in Albaugh et al. (1998). The other half was the non-fertilized reference (R). In 2005, the FACE plots were halved with a similar impermeable barrier and annual fertilization commenced in all plots (including FACEp) with only NH_4NO_3 at 11.2 g N m^{-2} on one half of each plot. Partitioning was done on an N–S or E–W axis such that each half had similar annual pine biomass increment and

litter production rates. The CO_2 and nutrient treatments created 16 plots consisting of four treatment plots each of aCO_2/no nutrient (AR), aCO_2/added nutrients (AN), eCO_2/no nutrients (ER) and eCO_2/added nutrients (EN).

2.2 | Root sampling

All aboveground mass from approximately 40% of each plot was harvested in early 2011 (Kim et al., 2020). Within each treatment plot, roots from one 'large' and 'small' diameter pine tree were excavated (32 trees total). Because of the cost in time and labour, lateral roots were not sampled at all depths in each treatment plot. First, all roots (pine and broadleaved) were carefully excavated in a 1.5 × 1.5 m pit (2.25 m^2) centred on each pine tree. All 32 trees were excavated to a depth of 30 cm. Sixteen of the trees (four from each treatment, one from each plot) were excavated to a depth of 60 cm, and four trees (one from each treatment) were excavated down to 90 cm. All coarse roots >2 mm in diameter were removed by sieving soil through 0.64-cm^2 mesh hardware screen. Following manual excavation, a backhoe was used to remove the entire taproot down to 120 cm, if necessary. To sample coarse roots outside the centre pit, a 65 × 75 cm (0.49 m^2) side trench was excavated diagonally at the corner of each pit to the sample depth of the pit. Lateral roots collected in the pits and side trenches were considered to belong to the target tree assuming that biomass of roots entering the pit or trench was equal to the biomass of roots exiting the pit (Jackson & Chittenden, 1981). Root harvests commenced on 2 May 2011 and were completed on 22 June 2011. Approximately 3200 person-hours were used to complete the excavations.

All roots were brought to the laboratory, washed with de-ionized water and separated into pine and broadleaved fractions. Pine roots were separated into taproot and lateral coarse roots, and pine and broadleaved roots were further separated into four diameter classes: 2–5, 5–15, 15–30 and >30 mm. All roots were dried to a constant weight at 65°C and weighed. When necessary, large roots were chipped to facilitate drying. Subsamples from each size class were ground and combusted in muffle furnace at 450°C to determine ash content.

2.3 | Pine root allometric equations and stand scaling

Separate allometric equations were developed for taproot and lateral root biomass using a simple power function,

$$B = a \times \left(D^2\right)^b, \tag{1}$$

where B is pine root biomass (kg $tree^{-1}$) of the taproot (B_{tr}) or lateral roots (B_{lr}), D^2 is stem diameter (cm) at breast height squared, and a and b are parameters to be estimated. Roots collected in the pit were used to parameterize Equation (1) for B_{tr}. Lateral root biomass for each tree was estimated for three concentric zones around each tree (Figure 1a). Roots collected in the pit were used to scale root biomass to the area of zone 1 as:

$$B_{lr_1} = P \times \frac{a_1}{2.25}, \tag{2}$$

where B_{lr1} is root biomass in zone 1, P is root biomass in the 2.25 m^2 pit (kg m^{-2}) and a_1 is the area of zone 1 (3.53 m^2). Roots collected in the trench were used to estimate root biomass in zone 2 as:

$$B_{lr_2} = T \times \left(a_2 - a_1\right), \tag{3}$$

where B_{lr2} is root biomass in zone 2, T is root biomass in the 0.49 m^2 trench (kg m^{-2}) and a_2 is the area of zone 2 (10.29 m^2). Lateral roots can extend up to 7 m from the stem depending on tree diameter (Gilman, 1990; Johnsen et al., 2005), well outside of the radius of zone 2 (1.81 m). To estimate lateral root biomass in this area (zone 3), we first estimated the maximum root area (MRA; i.e. root spread) for the tree as,

$$\mathrm{MRA} = 106.15 \times D^{1.18}, \tag{4}$$

where MRA is the area (m^2) occupied by roots and D is stem diameter (m) (modified from Roering et al., 2003). Root biomass in zone 3 was estimated from roots collect from the trench as,

$$B_{lr_3} = T \times \left(\mathrm{MRA} - a_2\right) \times \mathrm{CF}, \tag{5}$$

where B_{lr3} is root biomass in zone 3 and CF (0.2399) is a correction factor (Figure 1b) to account for biomass attenuation with distance from the edge of zone 2 to the edge of MRA. The correction factor was estimated from a normalized decay function derived from a relationship between root cross-sectional area (proportional to biomass) and distance from an inflection point (~1.3 m from the stem) representing a transition from mechanical support and transport function to only transport (R. Oren, unpublished data). Total lateral root biomass (B_{lr}) was estimated as the sum of B_{lr1}, B_{lr2} and B_{lr3}.

Equation (1) was applied to all trees in the plot to estimate plot-level root biomass (PB_r) (kg m^{-2}):

$$PB_r = \frac{\sum_{i=1}^{n} B_{tr_i} + \sum_{i=1}^{n} B_{lr_i}}{A_p}, \tag{6}$$

where B_{tri} and B_{lri} is root biomass in the pit for tree i in the plot containing n trees and A_p is treatment plot area (Table S1). Equation (6) was used to estimate pine taproot and lateral root biomass at soil depths 0–30, 30–60 and 60–90 cm and for taproot mass >90 cm. Plot root biomass in each soil layer was partitioned into size classes as the product of PB_{tr} or PB_{lr} and the proportion of each size class at that soil depth (Tables S4 and S5), where PB_{lr} was weighted by the proportion of root mass in each zone (Figure 1).

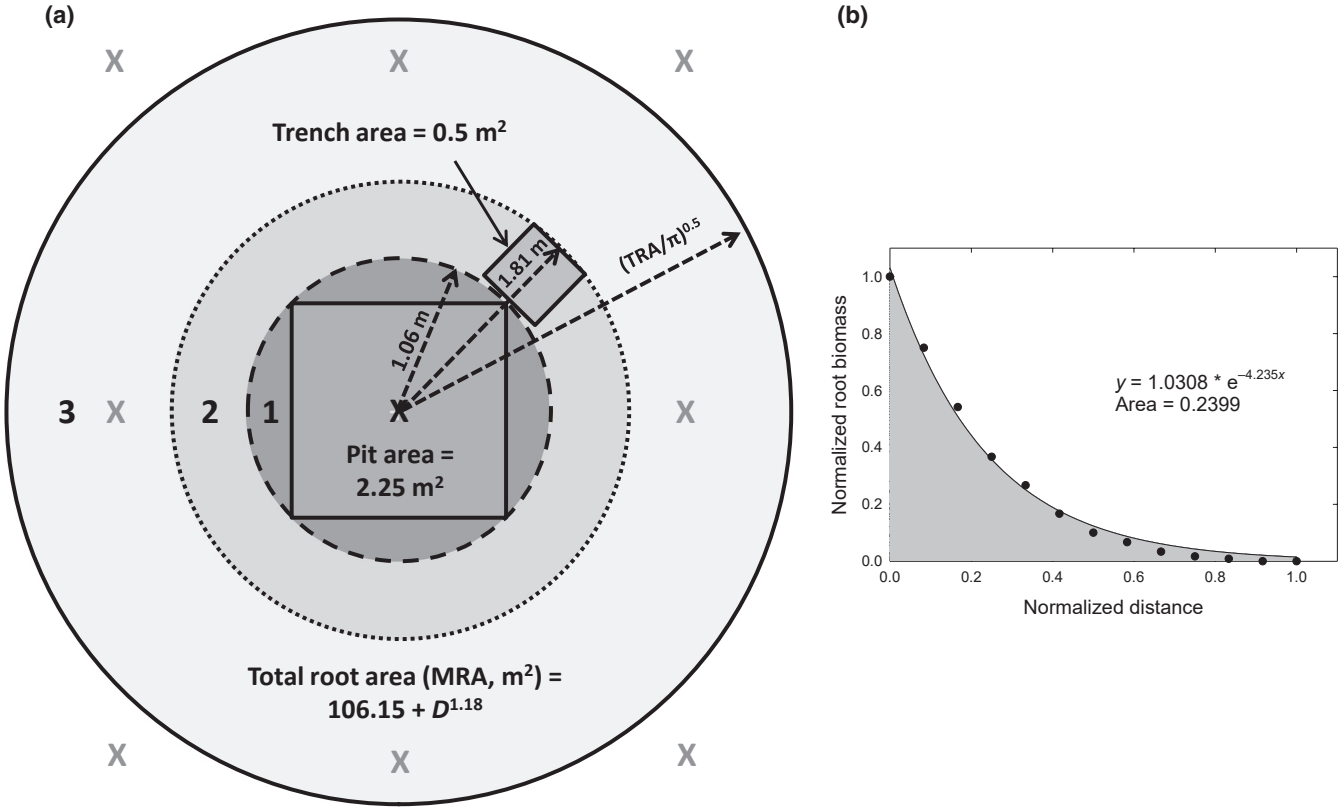

FIGURE 1 Approach for estimating total lateral root biomass from roots excavated in a 2.25 m^2 pit centred on the tree stem and a 0.49 m^2 side trench. The bold 'X' in the centre denotes the target tree and the grey 'X' are neighbour trees on 2.0 × 2.4 m spacing. Root biomass was determined for three zones. From the target tree, roots in zone 1 extend 1.06 m (area = 3.53 m^2) and in zone 2 extends to 1.81 m (area = 6.76 m^2). Roots in zone 3 extend to maximum root area (MRA, m^2), estimated as MRA = 106.15 × $D^{1.18}$, where D is tree diameter at breast height (m) (modified from Roering et al., 2003). For example, a 25 cm tree would have a MRA = 20.7 m^2 and roots would extend to 2.57 m. Roots excavated from the pit and trench were used to estimate biomass in zones 1 and 2 respectively. Biomass in zone 3 was estimated from the trench multiplied by a correction factor (b) to account for root biomass attenuation from the edge of zone 2 to the edge of MRA. The correction factor was estimated from a normalized decay function derived from a relationship between root cross-sectional area (proportional to biomass) and distance from an inflection point (~1.3 m from the stem) representing a transition from mechanical support and transport function to only transport (R. Oren, unpublished data)

2.4 | Broadleaved allometry and stand scaling

Broadleaved root biomass was estimated from roots sampled in the pine pits and side trenches. There was no relationship between broadleaved root biomass and pine stem diameter, so plot-level biomass proximal to the 2.25 m^2 pit (BB_{pr}) was determined as the product of the average between the two sample trees and the total pine tree count for the plot (Table S1). Broadleaved root biomass distal to the pit (BB_{dr}) was estimated using trench data multiplied by the plot area not contained in a pit (Table S1). Total plot broadleaved root biomass (kg m^{-2}) was estimated as,

$$BB_r = \frac{BB_{pr} + BB_{dr}}{A_p}. \quad (7)$$

Broadleaved root biomass in each soil layer was partitioned into size classes as the product of BB_{pr}, BB_{dr} or BB_r and the proportion of each size class at that soil depth (Table S6).

To estimate broadleaved root biomass through time, we used an allometric equation developed by Miller et al. (2006) for broadleaved competitors in a *P. taeda* plantation similar to ours in age, structure and soil type,

$$B_i = c \times e^{((\ln D \times a) - b)}, \quad (8)$$

where B_i is root biomass (kg) of tree i, ln$D$ is natural log(diameter) (cm), a = 1.921950652, b = 2.100356610 and c = exp(0.09344710/2). Plot-level broadleaved root biomass under aCO_2 (kg m^{-2}) was estimated as,

$$aB_{pred} = \frac{\sum_i^n B_i}{A_p}, \quad (9)$$

where n is the number of broadleaved trees in the plot (Table S1). We assumed broadleaved species had the same allometric relationship in all plots prior to CO_2 enrichment (year 0). Root biomass estimates were averaged across N treatments within a ring, because, as we show later,

there were no significant effects of N additions (beginning in 2005) on broadleaved root biomass. To account for the CO_2 effect on root biomass, we assumed a linear increase in the ratio of biomass between eCO_2:aCO_2 with time, and corrected the estimate of total broadleaved root biomass in each plot,

$$eB_{\text{pred}} = aB_{\text{pred}} \times \left(1 + k \times \frac{r-1}{n}\right), \quad (10)$$

where eB_{pred} is predicted broadleaved plot root biomass under eCO_2, k is the number years of CO_2 enrichment, r is the eCO_2:aCO_2 root biomass ratio (2.55, see Section 3 and Figure 6b), and n is the total number of years, which is 2 years longer in the prototype plot. Annual broadleaved tree inventories were used to estimate eB_{pred} through time (1996–2010).

2.5 | Biometric variables

Leaf area index (LAI) was estimated based on leaf litterfall samples, which was collected monthly (twice per month from October to January due to high volume) from 12 litter baskets (0.16 and 0.22 m^2 per basket before and after 2004) in each plot. Because the timing of leaf production and loss of *P. taeda* and broadleaved species were different, their LAI were estimated separately. Details of LAI estimation are given in McCarthy et al. (2007). Annual inventories of plot tree diameters as described in McCarthy et al. (2010) were used to estimate annual PB_r, aB_{pred} and eB_{pred} (1996–2010). Annual pine and broadleaved coarse root NPP was estimated with summed coarse root biomass increments of trees surviving 2 consecutive inventory years and ingrowth in the second year (Clark et al., 2001).

2.6 | Statistical analyses

The experimental design was a randomized complete block with a split plot where CO_2 and N amendments were the main and split-plot effects respectively. All statistical analyses were conducted in SAS (Version 9.3; SAS Institute Inc.). Treatment effects on pine allometric relationships (Equation 1) of B_{tr} and B_{lr} were tested for each soil depth and across all depths using the analysis of covariance (ANCOVA). In most cases, a natural log–log transformation of response and continuous variables was performed to correct for heteroscedasticity. A correction factor based on mean squared error was used to account for bias when log$B$ was back transformed to kilograms (Baskerville, 1972). Treatment effects on PB_{tr}, PB_{lr}, PB_r, BB_{pr}, BB_{dr}, BB_r and total coarse root biomass ($TB_r = PB_r + BB_r$) were analysed using ANOVA (PROC MIXED). Time series estimates of annual standing root mass and NPP were analysed by repeated measures ANOVA (PROC MIXED). A first-order autoregressive covariance structure (AR(1)) was selected based on AIC fit statistics. Individual plots were used as replicates. Block and Block × CO_2 were treated as random variables with plots blocked to the pairing of plots established at beginning of the experiment ($n = 4$). Significant treatment or interaction effects were further analysed using multiple comparisons of LSMEANs with Tukey's test. When necessary, plot pine basal area at the beginning of the study was used as covariate to account for variation in plot conditions at the beginning of the study.

ANCOVA was used to explore relationships between PB_r and BB_r and stand-level variables: basal area (BA), aboveground biomass and LAI. For this analysis, PB_r or BB_r was the dependent variable, CO_2 and N treatment combination (AR, AN, ER, EN) was the treatment, and pine or broadleaved BA or LAI was used as the quantitative linear covariate. Treatment effects on regression lines were tested using full and reduced models; first by testing the entire regression (i.e. intercepts and slopes simultaneously). If treatment was significant, then a separate analysis for differences in slope or intercepts was performed. Linear contrasts were used to test for differences between regressions and for making pairwise comparisons. To control Type I experiment-wise error, a Bonferroni correction was used to derive the appropriate significance level (α) when multiple comparisons were made (Zarnoch, 2009).

3 | RESULTS

3.1 | Pine diameter and biomass relationships

Pine taproot (B_{tr}) was significantly correlated with D^2 at all soil depths (Figure S1). There was no eCO_2 or N treatment effect on the relationship ($p > .05$) at any depth; therefore, allometric equations were developed for data pooled across all treatments (Table S2). Similarly, lateral root biomass (B_{lr}) was correlated with D^2, in the 0–30, 30–60 and 60–90 cm depths. In this case, eCO_2 significantly affected the relationship between B_{lr} and D^2 for roots in the top 30 cm ($p = .052$) (Figure S1b, Table S2). Treatment had no effect on B_{lr} in the 30–60 cm depth. Because only one tree per treatment combination was sampled at the 60–90 cm depth, treatment effects on B_{lr} could not be tested.

To simplify the estimates of total pine root biomass and calculations of NPP, allometric equations for B_{tr} and B_{lr} were developed for roots summed over all depths (Figure 2, Table S3). In this case, the relationship for B_{lr} for depths 30–60 and 60–90 cm (Table S2) was used to estimate lateral roots of harvested trees not sampled at that depth. When summed across depth, neither eCO_2 nor N affected the allometry of B_{tr}; however, the allometric relationship for B_{lr} differed with treatment ($p = .061$, Figure 2b). Trees with a similar diameter had greater B_{lr} under eCO_2 indicating a change in allometry. There was no significant bias in the normalized residuals for any of the regression models.

3.2 | Stand-level coarse root biomass

Plot-level pine root biomass was significantly increased under eCO_2 (Table 1). Elevated CO_2 increased total pine root mass (PB_r)

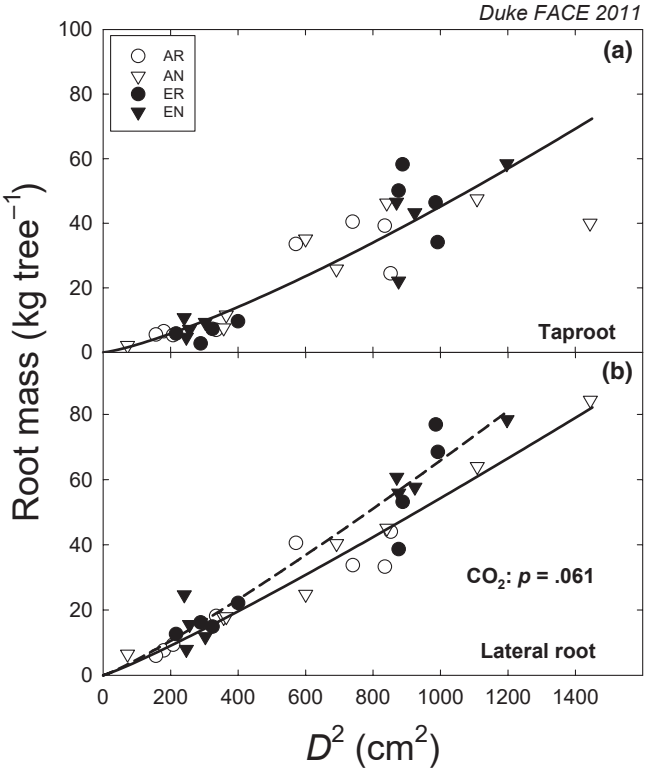

FIGURE 2 Pine coarse root biomass (kg tree^{-1}) versus tree diameter at breast height squared (D^2) for roots summed over 0–120 cm for taproot (B_{tr}) (a) and 0–90 cm for lateral roots (B_{lr}) (b). Symbols represent treatments (legend: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition), and each data point is an individual tree. In panel (a), the regression line is fitted to all treatments combined. In panel (b), the line is fitted to each CO_2 treatment

32.5 ± 4.4% or 1.80 kg m^{-2} above the 5.66 kg m^{-2} observed under aCO_2 (SE = 0.27, p = .007). Treatment response differed for taproot (PB_{tr}) and lateral root (PB_{lr}) fractions. Elevated CO_2 increased PB_{tr} by 0.53 kg m^{-2} or 22.5 ± 4.1%, over aCO_2 (2.43 kg m^{-2}, SE = 0.11, p = .013). In contrast, eCO_2 increased PB_{lr} 40.0 ± 4.7% (A: 3.23, E: 4.50 kg m^{-2}, SE = 0.13, p = .006). There was no significant N or CO_2 × N interaction on either root component.

Compared to pine, total broadleaved root biomass (BB_r) was 2.55 times higher under eCO_2 (A: 0.81, E: 2.06, SE = 0.24, p = .033) (Table 2). This increase was largely due to a significant CO_2 × N effect on broadleaved roots proximal to a pine stem (BB_{pr}) where the N treatment decreased root mass under aCO_2, but increased mass in eCO_2. There was no treatment effect on roots distal to the pine stem (BB_{dr}). Total root biomass (TB_r, pine + broadleaved) ranged between 5.65 and 11.12 kg m^{-2}. Elevated CO_2 increased TB_r by 47.9 ± 3.4% (A: 6.47, E: 9.52 kg m^{-2}, SE = 0.37; p < .001) (Figure 3). There was no significant N (p = .206) or CO_2 × N (p = .185) interaction on TB_r. The proportion of BB_r to TB_r was greater under eCO_2 (0.22) than under aCO_2 (0.13) (SE = 0.04, p = .001) (Figure 3, inset).

3.3 | Root size class distribution with depth

Pine root biomass declined asymptotically with depth for all size classes (Figure S2). For all size classes, 45%–75% of root mass in the profile was found in the 0–30 cm depth and less than 25% was found at depths 60–90 and >90 cm (Figure 4). Elevated CO_2 increased PB_{tr} and PB_{lr} in all root size classes (Table 3, Figure 4, inset). There was a significant CO_2 × N interaction for the 2–5 mm roots where N increased root mass under eCO_2 more than under aCO_2. There was

TABLE 1 Averaged pine tree diameter at breast height (dbh), stand-level basal area (BA, m^2 ha^{-1}), root, stem and total aboveground biomass (AGM = stem + branch + foliage), the ratio of root to stem (root:stem), the ratio of root to AGM (R/S) and results of ANCOVA. Total pine root biomass (PB_r) was partitioned into taproot (PB_{tr}) and lateral roots (PB_{lr}) summed over 0–90 cm soil depth. Biomass values are least square means (kg m^{-2}) and standard error (SE). Treatments are: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition

	dbh	BA	PB_r[b]	PB_{tr}	PB_{lr}	Stem mass[c]	AGM[c]	Root:stem	R/S	LAI
Treatment										
AR	21.12	47.02	5.42	2.32	3.10	21.1	23.5	0.258	0.231	3.55
AN	22.57	50.40	5.90	2.54	3.36	23.1	25.6	0.257	0.232	3.84
ER	24.44	55.96	7.40	2.94	4.46	27.9	30.9	0.267	0.241	4.19
EN	24.46	57.23	7.52	2.98	4.54	28.6	31.4	0.265	0.241	4.16
SE	1.18	1.72	0.27	0.12	0.15	1.8	1.9	0.008	0.007	0.19
Effect										
CO_2	0.029	0.012	0.007	0.013	0.006	0.030	0.030	0.234	0.146	0.001
Nitrogen (N)	0.482	0.125	0.176	0.195	0.169	0.181	0.241	0.745	0.915	0.251
C × N	0.493	0.451	0.398	0.355	0.444	0.488	0.477	0.882	0.869	0.147
Ipba[a]	ns	0.001	0.027	0.036	0.021	0.098	0.099	ns	ns	0.011

[a]Initial (1996) pine basal area. If 'ns', then p > .10 and ipba is not included in the model.

[b]$PB_r = PB_{tr} + PB_{lr}$.

[c]Stem mass and AGM are from Kim et al. (2020).

	BA	BB_{pr}	BB_{dr}	BB_r	AGM[b]	R/S	LAI
Treatment							
AR	6.77	0.35	0.62	0.99	1.67	0.67	2.53
AN	4.46	0.18	0.50	0.63	1.36	0.47	2.63
ER	7.40	0.81	1.17	2.02	2.07	1.01	2.70
EN	6.63	1.14	0.97	2.11	1.84	1.23	3.47
SE	1.01	0.13	0.50	0.29	0.43	0.19	0.21
Effect							
CO_2 (C)	0.270	<0.001	0.243	0.033	0.390	0.014	0.082
Nitrogen (N)	0.130	0.480	0.546	0.588	0.351	0.947	0.059
C × N	0.417	0.041	0.886	0.370	0.873	0.279	0.123
Ipba[a]	0.037	ns	ns	0.094	ns	ns	0.004

TABLE 2 Average broadleaved basal area (BA, m^2 ha^{-1}), coarse root biomass proximal (BB_{pr}) and distal (BB_{dr}) to a 2.25 m^2 area around a pine stem, total root biomass (BB_r), aboveground biomass (AGM), the ratio of root to AGM (R/S), broadleaved peak leaf area index (LAI) and results of ANCOVA. Biomass values are least square means (kg m^{-2}) and standard error (SE). Treatments are: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition

[a]Initial (1996) pine basal area. If 'ns', then $p > .10$ and ipba was not included in the model.
[b]AGM is from Kim et al. (2020).

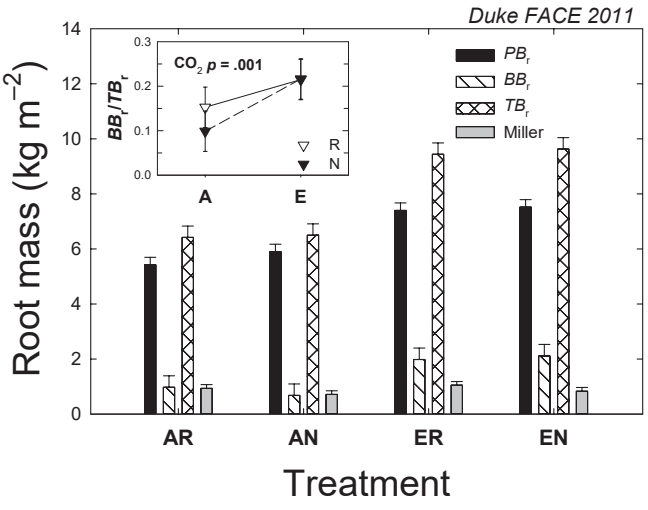

FIGURE 3 Stand-level pine (PB_r), broadleaved (BB_r) and total (TB_r) root biomass and the ratio of broadleaved to total root biomass (inset). The bar labelled 'Miller' are allometric estimates of broadleaved root biomass based on the equation from Miller et al. (2006). Data are least square means and standard errors ($n = 4$). Treatments are: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition

a strong CO_2 × depth interaction for all root categories, where significant effects of eCO_2 was limited to the 0–30 cm depth and at the 30–60 depth for roots >30 mm (Figure S2). Within the 0–30 cm depth, eCO_2 had a greater relative effect for PB_{lr} increasing root biomass 41%, 45%, 52% and 43% for 2–5, 5–15, 15–30 and >30 mm size classes, respectively, compared to 22% for PB_{tr}. There was also significant N × depth interaction for 2–5, 5–15 and >30 mm roots (Table 3); however, a consistent pattern across root categories was difficult to ascertain.

Broadleaved root biomass distribution was more variable than pine and showed a different distribution with size and soil depth under eCO_2. Under aCO_2, BB_r declined with depth (Figure S3) and the pattern was similar for all size classes. For the 2–5 mm size class, 64%, 32% and 4% of the root mass was in the 0–30, 30–60 and 60–90 cm depth respectively (Figure 5). For root sizes larger than 5 mm, >80% of the root mass was in the 0–30 cm soil depth. In contrast, under eCO_2, BB_r increased at the 30–60 cm depth relative to the 0–30 cm depth (Figure 5 and Figure S3). Summed over size classes, 54% of root mass was in the 30–60 cm depth compared to 41% in the 0–30 cm depth and <10% in the 60–90 cm depth. When summed over depth, eCO_2 increased BB_r in all root sizes (Table 3); however, in contrast to pine, a greater increase in biomass was observed for large roots (>15 mm, >3.5 times) than small roots (<2.1 times). The N treatment had no effect on BB_r or root distribution except for 15–30 mm size class (Figure S3). This was caused by a large broadleaved taproot in close proximity to a side trench in one of the ER plots. There were no significant N × depth or CO_2 × N × depth interactions for any size class.

3.4 | Root:Shoot ratio (R/S)

There was no significant CO_2 or N treatment effect on pine R/S (Table 1). Pine R/S ranged from 0.21 to 0.26 and averaged 0.236 ± 0.003. However, PB_r increased linearly with pine BA (Figure 6a), total AGM (Figure 7a) and LAI (Figure 7b). In all cases, PB_r, plots with similar BA, AGM or LAI carried more root biomass under eCO_2 indicating that CO_2 enrichment shifted biomass partitioning belowground.

Broadleaved root mass increased with BA (Figure 6b) and the slope of the relationship was greater under eCO_2. In contrast to pines, eCO_2 had no effect on aboveground broadleaved biomass. Thus, the large increase in BB_r under eCO_2 increased R/S from 0.572 under aCO_2 to 1.121 in eCO_2 (SE = 0.135) (Table 2). These relationships suggest broadleaved trees increased belowground allocation under eCO_2. Broadleaved BA ranged accounted for 10.5 ± 1.6% and 11.4 ± 2.1% of total plot (pine + broadleaved) BA, in aCO_2 and eCO_2 treatments respectively. However, the large increased in

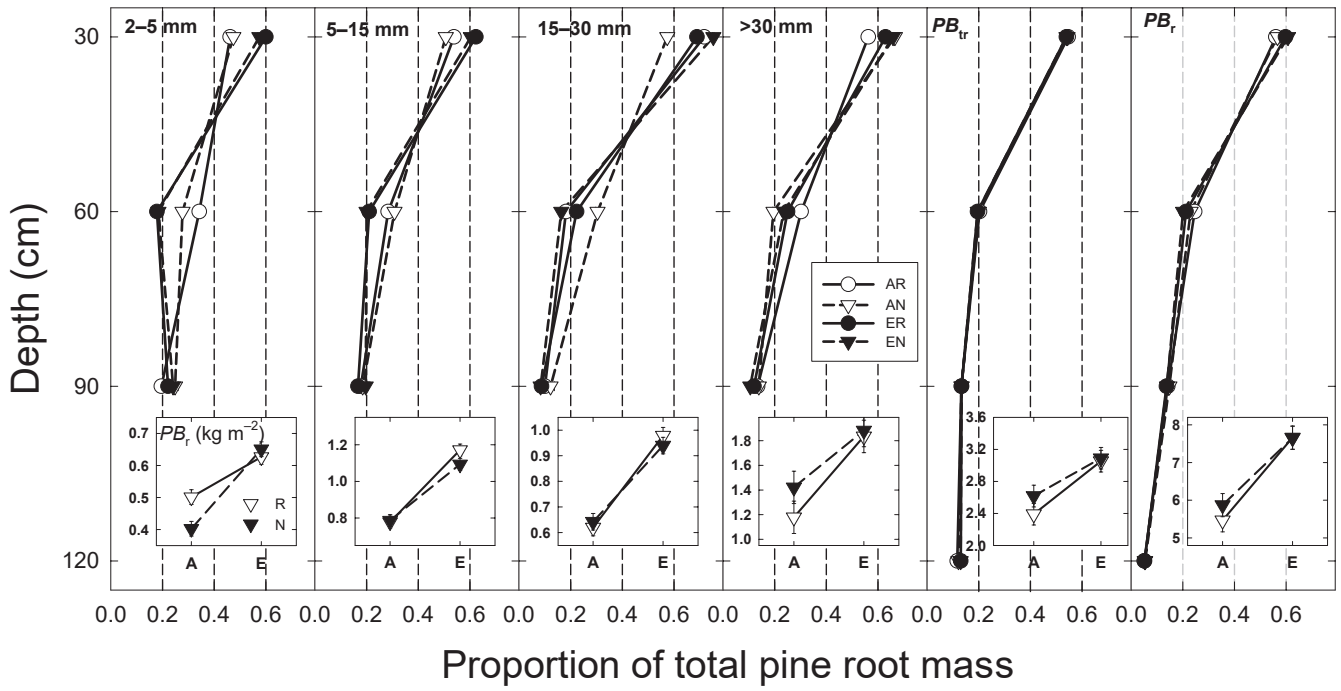

FIGURE 4 Relative distribution by depth of pine lateral root (PB_{lr}) by size class, taproot (PB_{tr}) and total root (PB_r) biomass. Symbols are the means and standard error ($n = 4$) for each treatment (legend: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition). Inset graph is PB_r summed over all depths in kg m^{-2} under ambient (A) or elevated (E) CO_2. Data are least square means and standard error. Statistics for the main panel and inset are in Table 3

broadleaved R/S under eCO_2 increased stand R/S 16.5 ± 3.1% (A: 0.249, E: 0.292; SE = 0.009; $p = .018$). There was no N or $CO_2 \times N$ effect on broadleaved or stand R/S.

3.5 | Coarse root net primary productivity

Pine root NPP under aCO_2 and eCO_2 was higher during the first 5 years of the study (1997–2001) compared to later years (Figure 8a). Comparing the AR and ER treatments over the study period (1997–2010), eCO_2 increased average pine root NPP by 49.4 ± 1.9% (E: 300.8, A: 202.7 g m^{-2} $year^{-1}$; SE = 17.3; $p = .010$). This led to a steady increase in the difference in PB_r between the CO_2 treatments ($CO_2 \times$ year: $p < .001$) (Figure 8b and Figure S4a). In contrast, mean broadleaved root NPP over the study period was much higher, 3.6 times greater under eCO_2 (E: 144.8, A: 38.8 g m^{-2} $year^{-1}$; SE = 19.0; $p = .013$) (Figure 8c). There was a significant $CO_2 \times$ year interaction in broadleaved NPP ($p < .001$) that led to an increasing difference in BB_r between CO_2 treatments (Figure 8d and Figure S4b). The annual pattern in total root NPP and TB_r was similar to pine with respect to eCO_2 (Figure 8e,f and Figure S4c). Elevated CO_2 nearly doubled the average total root NPP (E = 445.1, A = 241.0 g m^{-2}; SE = 17.4; $p < .001$). Nitrogen amendment (2005–2010) had no effect on broadleaved NPP but increased average pine NPP by 19.1 ± 3.6% (R: 222.8, N: 260.4 g m^{-2} $year^{-1}$; SE = 17.1; $p = .011$) and total root NPP by 15.0 ± 3.0% (R: 319.3, N: 361.6 g m^{-2} $year^{-1}$; SE = 11.7; $p = .009$). However, increased NPP from N additions had no effect on standing PB_r ($p = .135$) or TB_r ($p = .972$) by the end of the study (Figure 8b,f). There was no significant $CO_2 \times N$ effect on NPP or standing biomass for any root component.

4 | DISCUSSION

4.1 | Coarse root biomass and distribution with depth

Fifteen years of eCO_2 (17 years in FACEp) increased stand coarse root biomass (TB_r) by 3.08 kg m^{-2} over aCO_2 (6.46 kg m^{-2}), an increase of 48%. We hypothesized (**H1**) that long-term eCO_2 would increase TB_r, would alter root distribution with depth and that smaller diameter roots would be more sensitive to eCO_2 than large roots. Our data largely support this compound hypothesis; however, the response differed for pine and broadleaved components. The eCO_2 treatment increased pine coarse root biomass (PB_r) by 1.80 kg m^{-2} above the 5.66 kg m^{-2} observed under aCO_2, an increase of 32%. This is increase was due to both an increase in tree size (20.5%) and change in root allometry (12.0%). As expected, PB_r dropped precipitously with depth (Albaugh et al., 2006b) where 45%–75% of root biomass was found in the 0–30 cm depth and less than 25% was found at depths >90 cm. There was a significant $CO_2 \times$ depth interaction effect for all root size classes where increased biomass under eCO_2 was only significant at the 0–30 cm depth. At this depth, eCO_2 had a relatively greater effect on lateral roots (>41%) compared to taproots (<25%). Broadleaved trees accounted 13% and 22%

TABLE 3 Probability of significance (p-values) for treatment effects on pine (PB_r) and broadleaved (BB_r) root biomass with soil depth. Data for PB_r are partitioned into taproot (PB_{tr}) and lateral root (PB_{lr}) by size class. Data for BB_r are partitioned into size class

	Pine root size class					
	PB_r	PB_{lr}				PB_{tr}
		2–5 mm	5–15 mm	15–30 mm	>30 mm	
Effect						
CO_2 (C)	0.006	0.001	0.006	0.003	0.017	0.011
Nitrogen (N)	0.452	0.041	0.264	0.816	0.160	0.157
C × N	0.436	0.001	0.173	0.365	0.296	0.304
Depth (D)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
C × D	<0.001	<0.001	<0.001	<0.001	<0.001	0.004
N × D	0.806	0.037	0.060	0.444	<0.012	0.909
C × N × D	0.987	0.195	0.392	0.001	0.218	0.959
Ipba[a]	0.034	0.005	0.026	0.027	ns	0.039
Pine summed over depth						
CO_2 (C)		0.001	0.006	0.003	0.017	0.011
Nitrogen (N)		0.073	0.185	0.739	0.301	0.213
C × N		0.012	0.117	0.223	0.434	0.355
Ipba		0.005	0.023	0.026	ns	0.040
	Broadleaved root size class					
	BB_r	2–5 mm	5–15 mm	15–30 mm	>30 mm	
Effect						
CO_2 (C)	0.003	0.032	0.103	<0.001	0.003	
Nitrogen (N)	0.632	0.915	0.258	0.014	0.472	
C × N	0.896	0.446	0.337	0.128	0.905	
Depth (D)	<0.001	<0.001	0.003	0.015	0.001	
C × D	0.088	0.340	0.402	0.656	0.036	
N × D	0.836	0.682	0.661	0.489	0.489	
C × N × D	0.533	0.486	0.787	0.302	0.185	
Ipba[a]	0.019	ns	0.032	ns	0.026	
Broadleaved summed over depth						
CO_2 (C)	0.019	0.002	0.038	0.002	0.008	
Nitrogen (N)	0.710	0.843	0.089	0.023	0.245	
C × N	0.566	0.178	0.184	0.144	0.838	
Ipba	ns	ns	ns	ns	0.026	

[a]Initial (1996) pine basal area. If 'ns', then $p > .10$ and ipba was not included in the model.

of TB_r in aCO_2 and eCO_2 treatments respectively. Compared to the pines, eCO_2 had a much larger effect on broadleaved roots increasing BB_r by 255% (aCO_2: 0.81, eCO_2: 2.07 kg m^{-2}) and altered root distribution with depth. Under eCO_2, 54% of BB_r occurred in the 30–60 cm depth compared to less than 15% at the same depth under aCO_2. The reason for the large response at this depth is unknown, but competition with the dominant pine for space in the 0–30 cm depth may have precluded a large growth response at this depth or made investment in deeper roots more efficient. Contrary to our hypothesis, the increase in BB_r under eCO_2 was 3.5 times greater for large roots (>15 mm) compared to 2.2 times for small roots (<15 mm).

Comparison of root biomass among studies is difficult owing to different sampling methods, sampling depths and scaling (Addo-Danso et al., 2016). Our value for TB_r at age 30 under aCO_2 and no N (AR treatment) was 6.41 kg m^{-2} similar to the 6.24 kg m^{-2} reported by Miller et al. (2006) for a nearby 23-year-old *P. taeda* plantation receiving a similar site preparation treatment. In their study, broadleaved roots accounted for 12% of total root biomass compared to 11% in our study. In an earlier study at the Duke FACE site, Jackson et al. (2009) sampled coarse roots in 0.41 m^2 pits 32 cm deep. They did not report separated pine and broadleaved components. After 12 years of eCO_2 and 2 years of N amendment, coarse root biomass

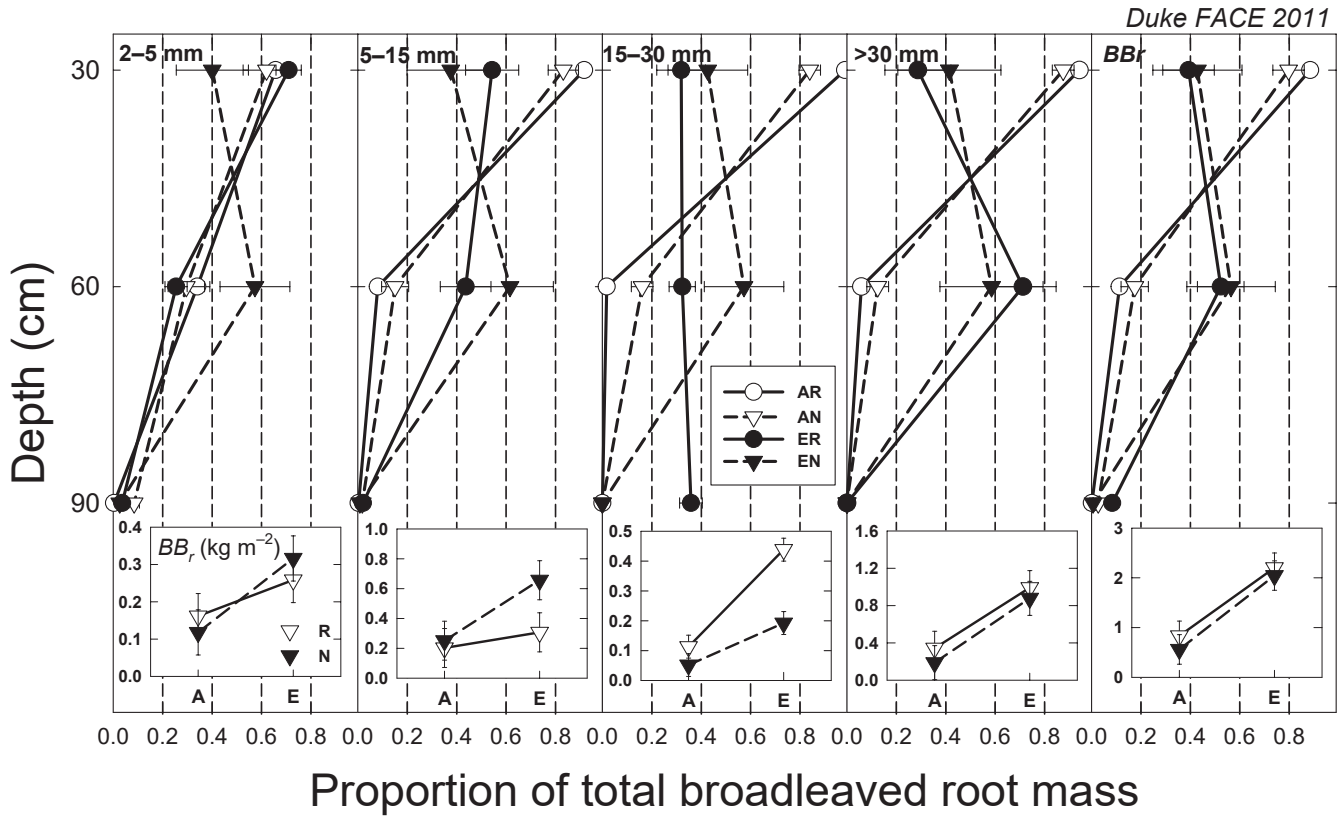

FIGURE 5 Relative distribution by depth of broadleaved root biomass by size class and total (BB_r). Symbols are the means and standard error ($n = 4$) for each treatment (legend: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition). Inset graph is total root biomass (BB_r) over all depths in kg m^{-2} under ambient (A) or elevated (E) CO_2. Data are least square means and standard error. Statistics for the main panel and inset are in Table 3

was approximately 0.3, 0.45, 0.65 and 1.05 kg m^{-2} in the AR, AN, ER and EN plots respectively. Comparing our raw trench data in the 0–30 cm depth, unadjusted for plot dimensions, our estimates were higher, 0.55, 0.78, 0.92 and 1.18 kg m^{-2} (SE = 0.17) for AR, AN, ER and EN plots respectively. Changes in stand development (2–3 years difference between studies) could explain higher biomass for our data. Differences in sampling methodology could also be a factor. For example, we sampled roots after all aboveground vegetation was removed and the randomly positioned trenches probably sampled a more representative portion of broadleaved roots as the trenches contained portions of taproots from small broadleaved and volunteer pines that were not sampled in the Jackson et al. (2009) study.

We found that smaller diameter pine lateral roots were more responsive to eCO_2 than taproots (hypothesis **H1c**). This response is consistent with increased fine root production and biomass observed at the Duke FACE site (Pritchard et al., 2008a; Taylor et al., 2014). Only a few studies have examined CO_2 effects on size class distribution of coarse roots. In young Norway spruce, 8 years of elevated CO_2 (2× ambient) had no effect on the primary root structure, but increased secondary roots growing on the primary roots by 58% (Pokorný et al., 2013). Jach et al. (2000) reported a 152% increase in total root biomass in young *P. sylvestris* following 3 years of elevated CO_2 (ambient +400 ppm) and that belowground dry matter partitioning was shifted towards small roots (≈7%). These studies support our observations for a larger relative increase in lateral root versus taproot biomass in pine. However, the opposite occurred for broadleaved roots. Functional equilibrium theory predicts an intrinsic linkage between leaves and fine roots (Cannell & Dewar, 1994). Thus, assuming a similar relationship with small broadleaved roots, the lack of a strong CO_2 response may be tied to little or no CO_2 response of broadleaved LAI (Kim et al., 2020). In this case, increased carbon supply from broadleaved photosynthesis (Ellsworth et al., 2012) under eCO_2 was allocated to coarse roots >15 mm.

4.2 | Root:shoot ratio (R/S)

We hypothesized (**H2**) that increased coarse root biomass under eCO_2 would be greater than that observed aboveground and would result in an increase in R/S. Our data partially support this premise. Pine R/S ranged from 0.21 to 0.25 under aCO_2, which is within the range reported in a meta-analysis of mature temperate coniferous plantations where AGM was greater than 150 Mg ha^{-1} (median R/S = 0.20; Mokany et al., 2006) and was similar to 0.24 reported for a nearby *P. taeda* plantation with a large broadleaved component (Miller et al., 2006). The 32% increase in PB_r under eCO_2 was larger than the 27% increase in AGM observed at the end of the study (Kim

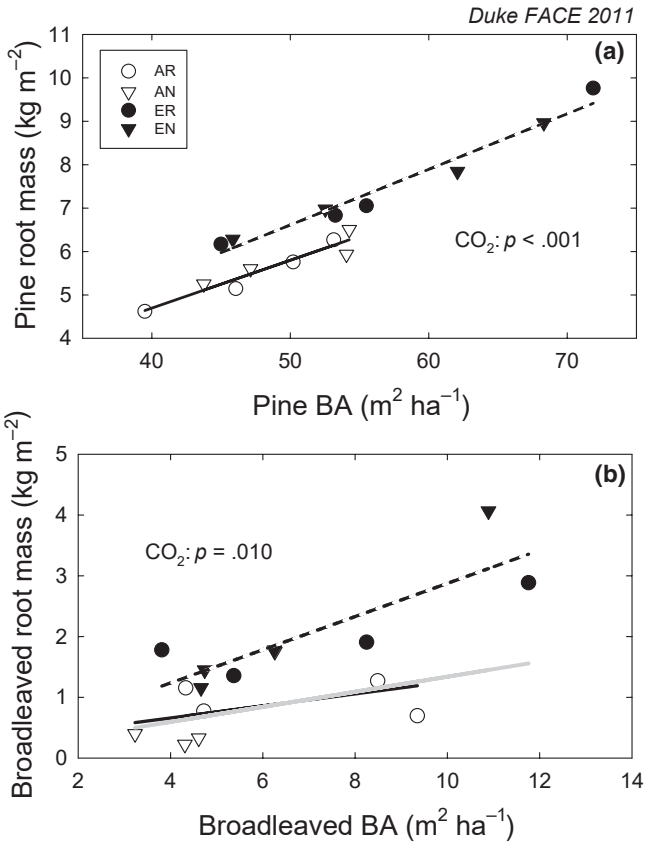

FIGURE 6 The relationship of pine root biomass (PB_r) and pine basal area (BA) (a) and broadleaved root biomass (BB_r) and broadleaved BA (b). Symbols are plot-level data where treatments are: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition. The solid black and dashed lines are regressions of the aCO_2 and eCO_2 treatments respectively. The grey regression line in panel (b) is the estimate of broadleaved root biomass in the aCO_2 treatment based on an allometric equation from Miller et al. (2006)

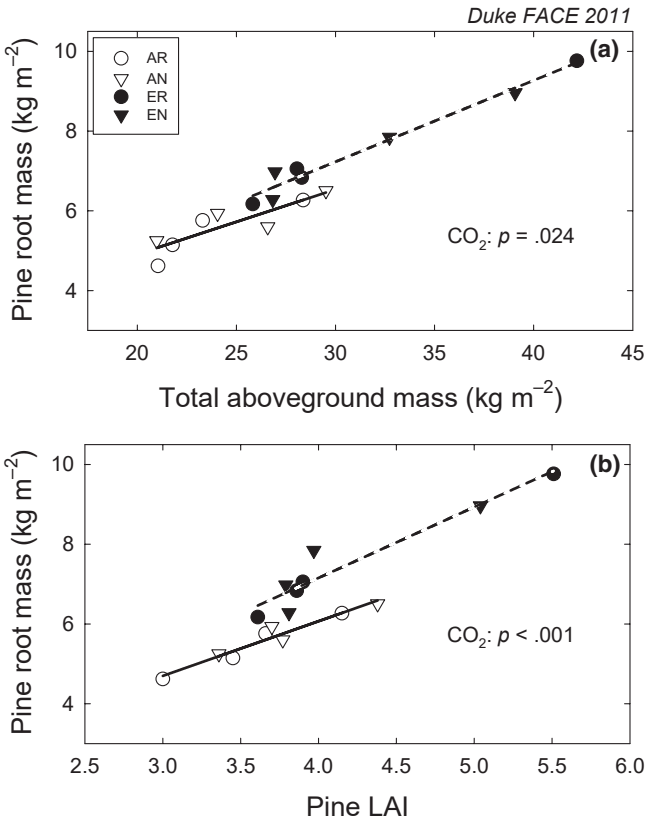

FIGURE 7 Relationship between pine root biomass (PB_r) and total aboveground pine biomass (stem + branch + foliage) (a) and PB_r and leaf area index (LAI) (b). Symbols are plot-level data where treatments are A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition. The solid black and dashed lines are regressions of the aCO_2 and eCO_2 treatments respectively

et al., 2020), although there was no significant CO_2 effect on treatment average R/S (p = .146). However, plot-level PB_r was strongly correlated with AGM (Figure 7a) and in plots with similar AGM, the eCO_2 treatments had greater root biomass. Our observations that eCO_2 had only small effects on pine R/S is consistent with studies that show alleviating soil resource limitations (i.e. nutrients and water), while greatly increasing growth of *P. taeda* does not strongly influence above/belowground biomass partitioning (Albaugh et al., 1998; Coyle & Coleman, 2005; King et al., 1999; Samuelson et al., 2004). In contrast to pine, eCO_2 increased broadleaved R/S from 0.57 to 1.12 and combined with pine increased stand R/S from 0.25 under aCO_2 to 0.29 under eCO_2 or 17%. Broadleaved trees were located primarily in the understorey, although there were a few large broadleaved trees that shared the canopy with the pine and may have had an overly large influence on the response to eCO_2. For example, we observed a CO_2 × BA interaction (Figure 6b) where the increase in BB_r with BA was greater under eCO_2. This interaction was likely caused by a few large broadleaved trees in two eCO_2 plots (accounting for 15.1% and 44.8% of plot broadleaved BA). We could not partition broadleaved overstorey versus understorey response to eCO_2, confounding species and canopy position.

Competition for light and soil resources is a major driver of carbon allocation to root and shoot tissues and may explain the large increase in broadleaved R/S relative to pine (Franklin et al., 2012). McCarthy et al. (2010) showed that increased aboveground NPP of pine under CO_2 enrichment was partly due to increased leaf area and was a function of soil nitrogen availability. We found a similar relationship between PB_r and LAI (Figure 7b), where for a given LAI, there was more PB_r in eCO_2. These data suggest that eCO_2 increased coarse root growth efficiency (i.e. root growth per unit LAI). Considering there was little change in R/S, increased PB_r was likely due to enhanced photosynthetic rate and not to whole tree shifts in carbon allocation. These results support a fixed structural biomass partitioning in this species that is not strongly affected by soil resource availability (Retzlaff et al., 2001) or eCO_2. Thus, isometric scaling of pine coarse root biomass from AGM (Figure 7a) is reasonable as long as AGM estimates account for CO_2 effects on root and aboveground allometry (Kim et al., 2020). In contrast, eCO_2 did not stimulate broadleaved AGM (Kim et al., 2020), hence, broadleaved R/S more than doubled under eCO_2. The lack of an eCO_2 effect on AGM is interesting as Schäfer et al. (2003) showed that

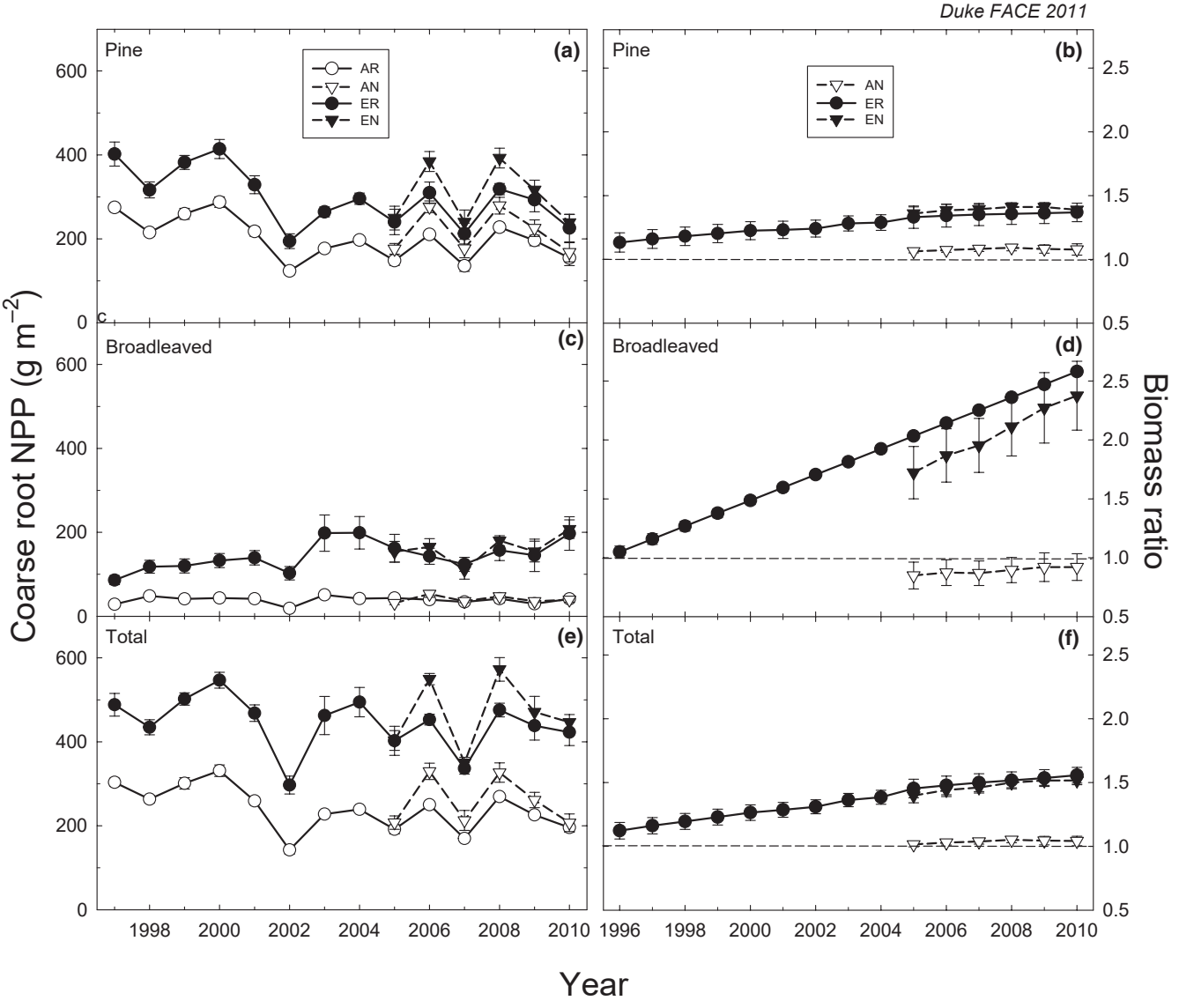

FIGURE 8 Time series of pine (a), broadleaved (c) and total (e) coarse root net primary productivity (NPP) and the ratio of pine (PB_r) (b), broadleaved (BB_r) (d) and total (TB_r) (f) biomass under AN, ER and EN to that under AR. Symbols are the means and standard error ($n = 4$) for each treatment (legend: A, ambient CO_2; E, elevated CO_2; R, native nitrogen; and N, nitrogen addition)

broadleaved canopy photosynthesis under eCO_2 increased 67%. In a light-limiting environment, optimal biomass partitioning theory (Franklin et al., 2012; Thornley, 1972) predicts a shift in partitioning away from roots to stems and vice versa under high light, thus a potential increase carbohydrate availability in eCO_2 being allocated to root biomass seems counter-intuitive. Alternatively, the observed response is consistent with the photosynthesis growth model proposed by Luo et al. (1994) that when the relative increase in plant photosynthesis under eCO_2 is greater than the relative increase in aboveground growth, the excess carbohydrate is allocated belowground to root growth. Kim et al. (2020) concluded that increased pine LAI (Kim et al., 2016) under eCO_2 reduced understorey light availability limiting aboveground broadleaved response to eCO_2. In addition, having to compete with a large increase in pine root biomass in the shallow, nutrient-rich soil (0–30 cm depth), increased belowground allocation in broadleaved root biomass was forced to deeper soil layers (Figure 5) that likely had lower available nutrients, further limiting aboveground growth response to eCO_2.

The large stimulation of broadleaved root biomass in the eCO_2 treatment has implications for estimates of biomass retention under long-term CO_2 enrichment (Walker et al., 2019) and modelling belowground carbon allocation (De Kauwe et al., 2014) particularly for the understorey vegetation. Additionally, increased allocation of biomass to broadleaved roots may confer better survival in shaded environments particularly under dry conditions, thus we may expect increased competition for soil resources under eCO_2. For example, increased root biomass per unit leaf area in pines and greater R/S in broadleaved species indicates an increase in root conductive area relative to leaf area, suggesting that trees growing under eCO_2 may have an advantage during periods of drought, perhaps because

larger coarse roots support more fine roots and a higher fine root surface area/leaf area ratio is hydraulically superior, especially under drought (Ewers et al., 2000).

4.3 | Coarse root NPP

We observed a sustained eCO_2 stimulation of pine and broadleaved root NPP over the 15-year study. While pine root NPP declined with time, the relative difference between eCO_2 and aCO_2 treatments was constant (≈49%). In contrast, broadleaved root NPP in eCO_2 increased with time relative to aCO_2. The combined pine and broadleaved root NPP (Figure 8e) under eCO_2 lead to a continuing expansion of TB_r relative to aCO_2 (Figure 8f). Elevated CO_2 stimulated the production and turnover of fine roots (Jackson et al., 2009; Pritchard et al., 2008a), mycorrhizal associations (Drake et al., 2011; Pritchard et al., 2008b), root exudates (Phillips et al., 2011) and litterfall (Lichter et al., 2008). This increased soil carbon flux may have stimulated microbial nitrogen cycling, and thus enhanced N availability under eCO_2 (Averill et al., 2015; Finzi et al., 2007) supporting greater above- and belowground NPP. Körner (2006) outlined three patterns for forest response to eCO_2 based on the degree of coupling with native soil capacity to supply resources for growth. The sustained increase in root NPP and continuing expansion of root biomass under eCO_2 suggest that this system still has sufficient nutrients to maintain a strong CO_2 effect on root growth (e.g. transitioning between Type II and Type III conditions, Körner, 2006) and the stands are not undergoing progressive nitrogen limitation observed in other forest FACE experiments (Norby et al., 2010).

4.4 | Response to N amendment

In the early FACEp study, Oren et al. (2001) showed that fertilization with balanced nutrients increased stem production under eCO_2 relative to the aCO_2 treatment. McCarthy et al. (2010) further showed that the magnitude of the stand NPP response to eCO_2 was a function of plot-level index of nitrogen availability (Finzi et al., 2007) mediated primarily through increased leaf area. Thus, we would have expected that plots with lower nitrogen availability to respond to N treatments. We found that N additions increased pine root NPP, and the response to N was additive in combination with eCO_2 (i.e. no significant $CO_2 \times N$). However, increased pine root NPP had no effect on final PB_r or TB_r, consistent with no observed N effect on AGM (Kim et al., 2020). Thus, we reject our hypothesis (**H3**) that root biomass response to eCO_2 will be enhanced by N additions. This contrasts with results of other belowground components where N treatment decreased fine root biomass and production (Jackson et al., 2009; Pritchard et al., 2008a), and increased fine root respiration (Drake et al., 2008) and soil CO_2 efflux (Kim et al., 2017).

We caution, however, that this conclusion must be taken in context of the experiment, that is mid-rotation *P. taeda* stands may have limited ability to respond to nitrogen fertilization. Response to fertilization varies widely dependent upon stand and site conditions, climate and type and rate of nutrient application. Increased production from fertilization is primarily mediated through increased LAI as increased foliar nitrogen concentration rarely results in a sustained increased in leaf photosynthesis in *P. taeda* (Fox et al., 2007a). Fertilization of the main study occurred when the trees were 25 years old when the crowns were closed. Response to fertilization of fully stocked mid-rotation *P. taeda* (where BA > 25 m^2 ha^{-1} and LAI > 3.5) may be limited if light and space are insufficient to support increased foliage biomass (Albaugh et al., 2006a; Fox et al., 2007a) or if foliar N concentration is near or above the critical level of 1.2% (Vose & Allen, 1988). Furthermore, in contrast to Oren et al. (2001), nitrogen-only fertilization was used in the main study. A fertilization response in *P. taeda* is dependent on nutrient application at the correct stoichiometric nutrient/nitrogen ratios (Albaugh et al., 1998; Fox et al., 2007b). For example, nitrogen additions reduced the foliar P/N ratio from 0.075 (SE = 0.004) in reference plots to 0.052 (SE = 0.002) (Aubrey Knier, unpublished data) well below the 0.10 considered adequate for growth (Albaugh et al., 2010). It is possible that the nitrogen-only fertilization used in this study disrupted the nutrient balance of trees, with adverse effects on growth (Oren et al., 1988).

4.5 | Uncertainties caused by coarse root biomass sampling and scaling

Measurements of root biomass in forest ecosystems are difficult and time-consuming and methods are generally not standardized (Addo-Danso et al., 2016). We used a combination of whole-root harvest in a central 2.25 m^2 pit and a subsample of lateral roots in a 0.49 m^2 side trench to estimate tree root biomass. This is a common approach for measuring root mass in *P. taeda* plantations where each tree is assumed to occupy a defined area based on planting density (in this study: 2.0 × 2.4 m spacing = 4.8 m^2 per tree) (e.g. Albaugh et al., 1998, 2006b; Maier et al., 2012; Samuelson et al., 2004). Allometric equations for pine taproot mass were robust. For example, a taproot equation developed for 8- to 12-year-old *P. taeda* growing in deep sandy soil (Albaugh et al., 1998) predicted stand taproot mass to within 1.5% of our estimates. Comparing estimates of lateral root mass is more problematic as the size of the central pit and pits between trees and sampling depth are usually different between studies. Lateral roots can extend several metres or more from the tree's stem (Gilman, 1990; Johnsen et al., 2005; Stone & Kalisz, 1991) much further than the edge of a typical centre pit. We accounted for this by predicting lateral root biomass as function of root spread based on tree diameter and root mass (Equations 2–5, Figure 1). The advantage of this approach is it allows for estimating total root biomass for each tree, proximal and distal to the central pit based on stem diameter and can be used to predict change in root biomass over time. An alternative approach for estimating PB_{lr} would be to scale root biomass in the 0.49 m^2 trench to all areas in the plot

not occupied by pine pit (A_{osp}, Table S1) (e.g. Albaugh et al., 2006b; Miller et al., 2006). This approach predicted 8.5 ± 0.8, 6.1 ± 1.2, 14.3 ± 1.5 and 8.9 ± 3.5% less root biomass in AR, AN, ER and EN, respectively, than our method. The difference was due in part to our estimate of root biomass in zone 3, which accounted for 5.5 ± 0.6% of PB_r.

Relative to the more intensive sampling of pine coarse roots, we measured broadleaved root mass using roots recovered in the pine pits and the proximity to a pine stem may have biased plot-level estimates of broadleaved roots . As a check on our estimates, we calculated broadleaved root biomass using an allometric equation developed by Miller et al. (2006) for broadleaved species growing in nearby (≈100 km) *P. taeda* stands similar to our study in age, soil type, and stand structure. The equation was applied to all broadleaved stems that had a measured dbh (Table S1). Using this equation, predicted broadleaved root biomass in the aCO_2 treatments was not significantly different from measured BB_r (Figure 3) and predicted values had a similar relationship with broadleaved basal area (Figure 6b). Accordingly, we feel our estimates of BB_r under aCO_2 are realistic, lending confidence that the observed large increase in biomass was a response to CO_2 enrichment.

Plot-level TB_r ranged between 5.65 and 11.12 kg m^{-2}, which corresponds to the upper range reported for temperate coniferous forests (Jackson et al., 1996). We likely captured all of the broadleaved roots, as there was little or no root mass in the 60–90 cm depths (Figure S4); however, for pine, 10%–20% of lateral roots were in the 60–90 cm depth, and consequently we may have underestimated R/S by not sampling below 90 cm (Robinson, 2007). Rooting depth is strongly influenced by soil physical and morphological characteristics and *P. taeda* roots can be found >200 cm (Albaugh et al., 2004). On another Piedmont site with a clay soil texture, *P. taeda* roots were found down to 170 cm, although roots below 90 cm accounted for only 2.2% of the total root mass (Albaugh et al., 2006b). Thus, we feel that our sampling accounted for most of the lateral pine roots.

4.6 | Implications

We found that long-term eCO_2 stimulated coarse root NPP and carbon accumulation in root biomass (48%) and that the magnitude of the response differed between dominant pine and broadleaved species. An accurate estimate of coarse root biomass response to eCO_2 is important as this pool sequesters carbon on-site for longer periods than aboveground biomass. Decomposing root systems provide many benefits to forests including biogeochemical cycling of nutrients, improved soil physical characteristic important for live root development and is a source for a large carbon flux into the soil matrix. Our stands were cut at age 30. Using a coarse root decay rate of 0.0534 $year^{-1}$ established for *P. taeda* in the Duke Forest (Ludovici et al., 2002), 21% or 1.19 and 1.57 kg m^{-2} of coarse root biomass in aCO_2 and eCO_2 treatments, respectively, would still be present after a subsequent 30-year rotation. This suggests that increased pine coarse biomass under elevated CO_2 would promote soil carbon sequestration over successive rotations assuming eCO_2 does not accelerate soil carbon cycling (De Graaff et al., 2006) or alter other factors that regulate long-term decomposition (Pendall et al., 2003).

Average overstorey pine R/S was not affected by eCO_2. These results suggest that isometric scaling from aboveground metrics (AGM, BA and LAI) may be acceptable for predicting coarse root biomass response to eCO_2 in closed-canopy pine forests; however, because of large increases in R/S in broadleaved species, isometric scaling would greatly underestimate root biomass of the understorey component and stand R/S. Our data on coarse root biomass under eCO_2 would be helpful for estimating stand carbon pools and allocation and for testing and constraining models predicting forest response to eCO_2.

ACKNOWLEDGEMENTS

Operated in cooperation with Brookhaven National Laboratory (K. Lewin and J. Nagy), the Duke Forest FACE project was supported by the Office of Science (BER) Terrestrial Ecosystem Sciences (TES) Program of US Department of Energy (DOE), under contract number DE-AC05-00OR22725, which also partially sponsored R.O. through DE-SC0006967. Financial support for Ram Oren was also provided by the Erkko Visiting Professor Programme of the Jane and Aatos Erkko 375th Anniversary Fund. The authors thank the many technicians who contributed in the field and laboratory throughout the duration of the Duke FACE project, particularly Karen Sarsony, Lance Kress, Robert Eaton and Tom Christensen for assistance in collecting and processing roots. This article was written and prepared in part by US Government employees on official time, and the textual content is therefore in the public domain and not subject to copyright.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Sampling and scaling design: Oren, Maier and Johnsen; Field sampling: Anderson, Oren, Palmroth, Maier, Kim and Johnsen; Root NPP data: Kim, Maier and Oren; LAI data: McCarthy and Oren; Data analysis: Maier and Oren; Writing: Maier. All authors provided comments on the interpretation and edited the manuscript.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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How to cite this article: Maier, C. A., Johnsen, K. H., Anderson, P. H., Palmroth, S., Kim, D., McCarthy, H. R., & Oren, R. (2021). The response of coarse root biomass to long-term CO_2 enrichment and nitrogen application in a maturing *Pinus taeda* stand with a large broadleaved component. *Global Change Biology*, 00, 1–19. https://doi.org/10.1111/gcb.15999