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RESEARCH ARTICLE

Increased leaf area index and efficiency drive enhanced production under elevated atmospheric [CO_2] in a pine-dominated stand showing no progressive nitrogen limitation

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Abstract

Enhancement of net primary production (NPP) in forests as atmospheric [CO_2] increases is likely limited by the availability of other growth resources. The Duke Free Air CO_2 Enrichment (FACE) experiment was located on a moderate-fertility site in the southeastern US, in a loblolly pine (*Pinus taeda* L.) plantation with broadleaved species growing mostly in mid-canopy and understory. Duke FACE ran from 1994 to 2010 and combined elevated [CO_2] (eCO_2) with nitrogen (N) additions. We assessed the spatial and temporal variation of NPP response using a dataset that includes previously unpublished data from 6 years of the replicated $CO_2 \times N$ experiment and extends to 2 years beyond the termination of enrichment. Averaged over time (1997–2010), NPP of pine and broadleaved species were 38% and 52% higher under eCO_2 compared to ambient conditions. Furthermore, there was no evidence of a decline in enhancement over time in any plot regardless of its native site quality. The relation between spatial variation in the response and native site quality was suggested but inconclusive. Nitrogen amendments under eCO_2, in turn, resulted in an additional 11% increase in pine NPP. For pine, the eCO_2-induced increase in NPP was similar above- and belowground and was driven by both increased leaf area index (L) and production efficiency ($PE = NPP/L$). For broadleaved species, coarse-root biomass production was more than 200% higher under eCO_2 and accounted for the entire production response, driven by increased PE. Notably, the fraction of annual NPP retained in total living biomass was higher under eCO_2, reflecting a slight shift in allocation fraction to woody mass and a lower mortality rate. Our findings also imply that tree growth may not have been only N-limited, but perhaps constrained by the availability of other nutrients. The observed sustained NPP enhancement, even without N-additions, demonstrates no progressive N limitation.

KEYWORDS
biomass, broadleaved species, FACE, free air carbon dioxide enrichment, loblolly pine, net primary production, *Pinus taeda*, site quality

1 | INTRODUCTION

Increased atmospheric [CO_2] may result in higher net primary production (NPP) of forest ecosystems. Understanding when the extra carbon (C) fixed under elevated [CO_2] (eCO_2) is used for foliage production, thus increasing the amount of photosynthetic machinery, or to wood, thus supporting long-term C sequestration, is key to predicting how forests will function, and how much and how fast C will move between biosphere and atmosphere in future climates (De Kauwe et al., 2014; Walker et al., 2019). Both the magnitude of NPP response and its partitioning may vary with C limitation to growth relative to that imposed by other resources (Ellsworth et al., 2017; Franklin et al., 2012; Körner, 2006; Maier et al., 2022; McCarthy et al., 2010; Norby et al., 2010; Oren et al., 2001; Sigurdsson et al., 2013). For example, based on a global meta-analysis on nitrogen (N) mediated growth responses, eCO_2 increased tree biomass production by 32% overall; but responses of trees fertilized with N was higher (40%) than of those not provided with N (24%; Wang & Wang, 2021). Earlier findings at the Duke Free Air CO_2 Enrichment (FACE) experiment also indicated that the initial production enhancement under eCO_2 was maintained only under balanced nutrient additions (Oren et al., 2001) and varied spatially with native site quality (McCarthy et al., 2010). However, excluding the recent study on coarse roots (Maier et al., 2022), the effects of long-term N-additions on NPP and its partitioning among organs at this site have not yet been quantified.

Dynamics of accumulation live biomass of trees over stand development (Bormann & Likens, 1979) is the outcome of production of all organs and turnover of some (leaves, branches, fine roots, and non-lignified reproductive organs) and the recruitment and mortality of individual trees (curve 1 in Figure 1). Increased resource supply or improved climate may elevate the steady-state biomass is approaching (M_{Pot}; curve 2), the rate at which biomass increases toward M_{Pot} (curve 3), or both (curve 4; see Groninger et al., 1999). Leaf biomass (or leaf area) shows similar dynamics but reaches a steady state much earlier than total biomass (Vose et al., 1994). Nutrient additions increase biomass accumulation rate (Albaugh et al., 2004; Trichet et al., 2008; Vose & Allen, 1988) and forests growing on better quality sites accumulate more biomass faster (curve 4; Samuelson et al., 2008; Vicca et al., 2012). In older stands, higher M_{Pot} (curve 2) may be possible where increased resources prolong positive net biomass increment. In accruing stands, a directional climate change (increase in temperature), management (fertilization) or experiments (CO_2 enrichment), may result in both greater biomass accumulation rates and projected M_{Pot}. It has been argued that CO_2 fertilization effects on tree/stand growth are most likely realized in young stands or on forest edges, where solar energy and soil resources are not fully utilized (Körner, 2006, 2022) and the primary growth response to eCO_2 is accelerated stand development (curve 3). However, if eCO_2 enhances carbohydrate availability and facilitates acquisition or utilization of additional resources, both biomass accumulation rate and M_{Pot} may increase (curve 4).

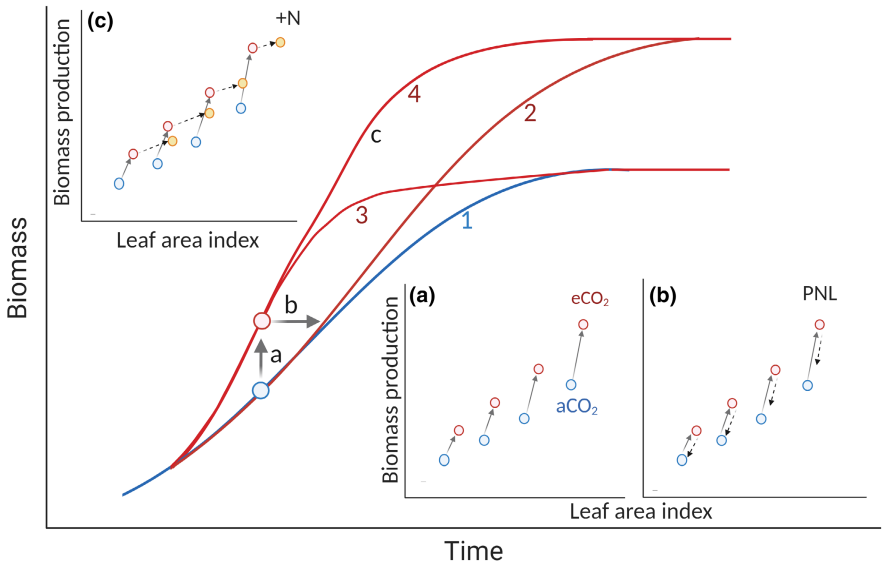

FIGURE 1 Typical accumulation of live biomass in a forest stand, in a given environment, reflecting the difference between biomass growth and mortality (curve 1). Increased resource supply may increase the theoretical steady-state biomass (curve 2), the rate at which biomass increases toward steady state (curve 3), or both (curve 4). Note that the dynamics of biomass accumulation are shown for total biomass; foliage biomass shows similar trajectories but peaks earlier in time than total biomass. Letters a, b, and c in the main figure refer to the insets that show potential growth responses to elevated atmospheric [CO_2] (eCO_2) and nitrogen-additions (+N) across a range of leaf area index (*L*) values reflecting native site quality. Initial growth enhancement under eCO_2 (grey arrows, red symbols) relative to stands growing under ambient conditions (aCO_2; blue symbols) is mediated by both an increase in *L* and in growth per unit *L* with overall enhancement increasing with site quality (a). Progressive nitrogen limitation (PNL) where the initial enhancement is diminished over time (dashed black arrows; b). Nitrogen-additions may restore or increase the eCO_2-induced growth enhancement (dashed black arrows, yellow symbols; c).

Response to increasing resource availability may include greater carbohydrate production per unit leaf area index (*L*) and/or a change in allocation of C between below- and aboveground. Fertilization on low fertility sites results in increased *L* and increased stem growth rate at comparable *L* (Albaugh et al., 2004). The primary reason for higher carbohydrate availability is an increase in *L* and canopy photosynthesis (Cannell & Dewar, 1994; Linder, 1987). However, as *L* increases in closed canopies, light interception increases proportionally less, and mean photosynthetic rate and production per unit *L* decrease (Norby et al., 2005; Vose & Allen, 1988; Waring, 1983). Because fertilization-induced enhancement of leaf photosynthetic rate can be small and/or transient (Maier et al., 2008), increased stem wood production per unit *L* may mostly reflect increased fraction of carbohydrates used aboveground (Axelsson & Axelsson, 1986; Haynes & Gower, 1995). Similarly, from purely eco-physiological standpoint, the response of biomass production to eCO_2 reflects the net effects of a potential increase in photosynthetic rate at a given *L*, its change with increasing *L*, and changes in C allocation, all of which can be affected by nutrient supply (inset a, Figure 1; blue symbols represent different pre-treatment "base *L*" and native site quality and red symbols hypothetical responses to eCO_2).

When soil nutrient availability limits biomass production, the extra carbohydrates produced under eCO_2 may not be partitioned to biomass but to fast-turnover C pools (e.g., root exudates), in effect speeding up the 'atmosphere-to-atmosphere' cycling of CO_2 and decomposition of soil organic matter (Palmroth et al., 2006; Phillips et al., 2011; Prescott et al., 2020). Put differently, if tree growth is mostly N-limited, then following an initial, eCO_2-induced, accelerated growth, reflecting increased N-uptake and/or -use efficiencies, soil N-availability becomes progressively limiting as N accumulates in plant biomass and soil organic pools (inset b; downward arrows indicate 'Progressive Nitrogen Limitation', PNL; Luo et al., 2004). By extension, under these circumstances, the steady-state *L* is not affected by eCO_2, but N fertilization (inset c; yellow symbols) may restore, and potentially increase, the eCO_2-induced growth enhancement. However, growth enhancement may be sustained even in the absence of nutrient additions as increased C flux belowground under eCO_2 may increase root production, rooting depth, and rhizosphere C deposition, priming decomposition of older organic matter (Drake et al., 2011; Iversen, 2010; Maier et al., 2022; Norby et al., 2004). These processes may improve access to previously untapped nutrient resources, leading to 'progressive release from N limitation' (Walker et al., 2015).

Free air CO_2 enrichment (FACE) experiments enable evaluation of eCO_2 effects, and their interaction with other climatic factors, on ecosystem structure and function, thus providing insights into the mechanisms underlying the response. Norby et al. (2005) demonstrated that, while the increase in NPP under eCO_2 was similar among FACE sites in young forests, the role of structural changes (increases in *L*) in driving the response decreased with increasing degree of canopy closure. Some FACE experiments in closed canopy and/or mature forests showed the expected strong coupling between eCO_2-induced enhancement of NPP and soil nutrient availability. For example, in a closed-canopy sweetgum (*Liquidambar styraciflua*) plantation, the initial growth enhancement under eCO_2 was manifested as higher light-use efficiency (NPP/amount of absorbed solar energy; Norby et al., 2005), but there was no long-term eCO_2 effect on NPP, and growth was deemed N-limited (Norby et al., 2010, 2022; Norby & Zak, 2011).

Duke FACE in a loblolly pine (*Pinus taeda* L.) plantation with broadleaved species found in the mid-to-lower canopy, was the longest-running FACE experiment to date (1994–2010) and the first to incorporate CO_2-by-nutrient interaction into the experimental design (Oren et al., 2001). Nutrient additions at this site were superimposed onto variation in native site quality that resulted from minor topographical variations that generated subsurface flows (Schäfer et al., 2002) and were associated with differences in soil depth and rock content (McCarthy et al., 2010). Compared to the slightly elevated northern and southern portions of the site, the shallow valley in the middle supported higher pre-treatment growth rate and pine *L* (L_P; Oren et al., 2006). Although the initial L_P was related to N-mineralization rate, likely reflecting the availability of other nutrients as well, some of the plots with higher N-mineralization rate were also located at lower elevations with deeper soils and greater water supply (McCarthy et al., 2010; Schäfer et al., 2002).

Based on earlier studies from Duke FACE, eCO_2 increased leaf photosynthesis (Ellsworth et al., 2012), canopy photosynthetic production (Schäfer et al., 2003), and had no direct effect on canopy transpiration (Domec et al., 2009; Tor-Ngern et al., 2015; Ward et al., 2018). Stand *L* increased and, after canopy closure, remained 19% higher under eCO_2 (Tor-Ngern et al., 2015), while the increase in stand NPP over the first decade of the experiment averaged at 27% (McCarthy et al., 2010). Notably, the magnitude of the eCO_2-induced enhancement of *L* and NPP varied with soil N availability among plots (Finzi et al., 2002; McCarthy et al., 2007, 2010). Elevated CO_2 increased total C flux belowground while N-additions under eCO_2 decreased it (Butnor et al., 2003; Drake et al., 2011; Jackson et al., 2009; Kim et al., 2017; Oishi et al., 2014; Palmroth et al., 2006). Fine-root NPP was 25% and biomass 24% higher under eCO_2, and N-additions under eCO_2 resulted in a 13% decrease in fine-root biomass (Jackson et al., 2009; Pritchard et al., 2008). By the end of the CO_2-enrichment period, aboveground pine biomass was 27% higher under eCO_2, with no apparent interaction with N-supply, while that of broadleaved species was similar across treatments (Kim et al., 2020). Coarse-root biomass of pine and broadleaved species were 32% and 155% higher under eCO_2, respectively, while the effect of N-additions on this quantity was small (Maier et al., 2022). That the effect of N-additions was obvious on fast-turnover C pools but not on woody biomass is not surprising given that any addition to woody biomass is made to an already large and continuously accumulating pool.

Taken together, the native nutrient supply at Duke FACE was sufficient to sustain a substantial eCO_2 effect on NPP and standing biomass perhaps by allowing access to deeper and/or previously inaccessible nutrient pools in the soil (Drake et al., 2011; Maier et al., 2022; McCarthy et al., 2010). However, the recovery

of eCO_2-induced growth enhancement in the FACE prototype upon balanced nutrient fertilization (Oren et al., 2001) and the limited NPP response to eCO_2 in the low N-availability plots earlier in the study (McCarthy et al., 2010), put in the context of the prevailing N-limitation (Hungate et al., 2003; Luo et al., 2004), suggest N-limitation to growth. Yet, the effects of N-additions on biomass production have not been assessed so far.

We assessed the $eCO_2 \times N$ effect on NPP (biomass production), by species group and organ, using a dataset extending 2 years beyond the termination of enrichment. We tested the following hypotheses: As projected based on the first 10 years of the experiment (McCarthy et al., 2010), eCO_2 will increase NPP more, and the enhancement ratio will be higher, in plots of higher native site quality (initial *L*) (H1). The effect of eCO_2 on NPP will be ephemeral in plots of low *L*, suggesting PNL (H2). Nitrogen-additions will counter PNL (H3). Higher NPP under eCO_2, with or without N-additions, is driven by increases in both *L* and production efficiency (PE = NPP/*L*); while PE is expected to decrease as *L* and within-canopy shading increases (H4). Nitrogen additions under eCO_2 will change allocation of NPP (from below- to aboveground organs) rather than increase total production (H5). In addition, we expected the NPP response of broadleaved species to reflect a direct response to eCO_2 and N-additions and, perhaps even more, an increased light limitation imposed by the response of pine *L* (Kim et al., 2016). Post-eCO_2 enrichment, we expected pine NPP to decline in proportion to that in *L* (Kim et al., 2017).

2 | MATERIALS AND METHODS

The Duke FACE experiment was in the Blackwood Division of the Duke Forest in Orange County, NC (35°97′ N, 79°09′ W). The tract was homogeneous, relatively flat with moderately fertile soils (Oren et al., 2006). The site characteristics are described earlier, for example, in Maier et al. (2022) and an abbreviated description is provided here. The experiment was set up in a 90-ha loblolly pine (*Pinus taeda*, L.) stand planted in 1983 at 2.0 × 2.4 m spacing following a chop-and-burn site preparation treatment. Individuals of 40 woody species, most commonly sweetgum (*L. styraciflua* L.), winged elm (*Ulmus alata* Michx.), dogwood (*Cornus florida* L.), and red maple (*Acer rubrum* L.) were found in the mid-to-lower canopy. Broadleaved species comprised 11% of basal area in 2010. The climate is warm and humid in the summer and moderate in the winter with a mean annual temperature of 15.5°C. Mean annual precipitation is 1145 mm. The soils are predominantly Enon silt-loam, characterized as moderately low fertility acidic clay-loam. Soil pH is ~6.0, and foliar concentrations of nitrogen (N; ~1.1%) and phosphorus (~0.3%) are average for mid-rotation loblolly pine stands in the region (Albaugh et al., 2010).

The FACE experiment consisted of eight circular experimental plots (30 m in diameter). A prototype ($FACE_P$) plot with an elevated [CO_2] (eCO_2) and a reference plot with ambient [CO_2] (aCO_2) were established in 1993, and six plots (three eCO_2 and three aCO_2; replicated FACE) were added 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 (Hendrey et al., 1999). Enrichment commenced in 1994 at $FACE_P$ and 1996 (at the end of the growing season) at FACE.

In 1998–2004, the $FACE_P$ plots received nutrient additions. Each plot was split in half by an impermeable barrier down to 70 cm and one-half of each plot was fertilized annually. Based on foliar nutrient analysis, the N application rate was set to either 5.6 or 11.2 g N m^{-2} (as NH_4NO_3 or urea) balanced with other nutrients (Albaugh et al., 1998). In 2005, the rest of the FACE plots were halved, and annual fertilization commenced in all plots (including $FACE_P$) with only NH_4NO_3 at the rate of 11.2 g N m^{-2} on one-half of each plot. In the analyses on N-addition effects, we included data collected from the replicated FACE (2005–2010). We were unable to detect a legacy effect of the earlier balanced nutrient additions in the data from the original $FACE_P$ plots. The CO_2 and N-additions created 4 × 4 half-plots representing four treatment combinations: aCO_2 (AR), aCO_2 + N (AN), eCO_2 (ER), and eCO_2 + N (EN). The experimental unit was a 'whole plot' through 2004, and a 'half-plot' from 2005, both referred to as 'plot'. The treatments continued through October 2010. Trees in one half of each plot, consisting of a quarter plot of each N treatment, were harvested in early 2011 and trees in the other halves were left intact for two more years (2011–2012) for continuous measurements (Kim et al., 2020). All the data used in this paper are publicly available (Oren et al., 2023).

2.1 | Environmental variables

Air temperature and relative humidity were measured in the upper third of the canopy in each plot (Vaisala HMP35C and HMP45C; Helsinki, Finland). On the central tower above the canopy of plot 4, a sensor (Q190; LiCor, Lincoln, NB, USA) for measuring photosynthetically active radiation and an automated system (tipping bucket TR-525USW; Texas Electronics, Dallas, TX, USA) for measuring precipitation were mounted. All sensors were sampled every 30 s, and 30-min averages were logged (CR21X or CR23X; Campbell Scientific, Logan, UT, USA). Beginning in 1997, volumetric soil water (θ; m^3 water m^{-3} soil) of the upper 30 cm soil layer was measured continuously at four locations in each of the replicated FACE plots, and from 2001 in the $FACE_P$ plots using various sensors (Campbell Scientific, Logan, UT, USA, and Delta-T Devices, Cambridge, UK). Soil moisture estimates for each sensor were rescaled to measured porosity (representing saturated water content) and hygroscopic minimum (Oishi et al., 2008).

2.2 | Estimates of leaf area index and NPP

As described in McCarthy et al. (2007) leaf production (all biomass production estimates are given as dry mass, g m^{-2} $year^{-1}$) and projected leaf area index (*L*, m_L^2 m_G^{-2}) were estimated using leaf litterfall samples collected bi-weekly/monthly from 12 litter baskets (0.16 or

0.22 m^2) in each plot. For our analysis, pine leaf litterfall data prior to 2004 were available only from six of the eight plots, and pine *L* estimates for those plots/years were taken from McCarthy et al. (2007, 2010). For broadleaved species, peak *L* was estimated as total annual leaf litterfall mass (leaf production) multiplied by specific leaf area ($m^2 g^{-1}$). For pine, to account for leaf longevity of ~19 months, *L* estimates were based on 2 years of litterfall (McCarthy et al., 2007, 2010). Reproductive biomass and production were also estimated based on litterfall collections (McCarthy et al., 2010).

Annual tree diameter and height measurements, combined with allometric relationships developed for trees and root systems harvested in 2011 (Kim et al., 2020; Maier et al., 2022), were used to estimate woody biomass and biomass production of each tree (stem, branches, and coarse roots [>2 mm diameter]). Woody biomass production represents our longest time series (covering all plots). Branch production estimates included branch biomass turnover, calculated based on annual measurement of the height of the base of live crown and vertical branch biomass distribution. For pine, biomass from individual branch sampling and whole-tree branch diameter measurements of harvested trees were used to calculate vertical branch biomass distribution. For broadleaved species, the branch biomass was vertically distributed into three parts (top, middle, and bottom crowns) as whole-tree branch diameter measurements were not available. We used previously published estimates of fine-root biomass and production (Jackson et al., 2009; Pritchard et al., 2008) and partitioned stand-level estimates between species groups based on coarse-root estimates. Allocation ratios were calculated as each component NPP divided by the sum of all components. Mortality rate (% $year^{-1}$) was calculated as: $\text{Mortality} = (N_{ref1} - N_{ref2})/N_{ref1} \times 100/\text{interval}$, where N_{ref1} is the number of reference trees in year 1 and N_{ref2} is the number of the reference trees survived until year 2.

Two estimates of annual biomass production (Clark et al., 2001) were calculated: (1) annual change in the biomass pool ($\Delta M = M_2 - M_1$), where M_2 and M_1 are live biomass in year 2 and year 1, respectively, and (2) NPP calculated for trees that are alive during two consecutive, annual inventories plus ingrowth (recruitment of individuals reaching the minimum measurable size) during the period. That is, ΔM represents net biomass increment (accounting for mortality), while NPP denotes biomass production of living trees. Our analyses focused mainly on the NPP estimates and the role of *L* versus PE (PE = NPP/*L*, where NPP is total NPP for each species group) in driving NPP. To explore the potential effects of stand developmental stage on biomass production, we also performed a classical growth analysis (Evans, 1972). We calculated relative growth rate as $\text{RGR} = \ln(M_2) - \ln(M_1)$, its determinants, leaf area ratio (LAR = *L*/*M*) and biomass increment per unit leaf area (unit leaf rate, ULR = $\Delta M/L$), and compared those at a common live biomass (a proxy for tree size) across treatments.

Enhancement ratios for each component, woody NPP (NPP_W; stem, branches, and coarse roots), ANPP, NPP, and *L* were calculated as 'X' at eCO_2/'X' at aCO_2 for each plot pair (based on the pairing of plots, i.e., each eCO_2 plot to an aCO_2 plot in the experimental design). To estimate annual enhancement, we averaged the plot-specific ratios ($n = 4$) and calculated standard error (SE). In addition, we calculated an enhancement ratio (at a standard *L*) for NPP_W based on the relationships between NPP_W and site quality under aCO_2 and eCO_2. The ratio was computed as actual NPP_W under eCO_2 divided by its expected value at the same *L* but under aCO_2. If no relationship under aCO_2 was found, mean NPP under aCO_2 was used as the expected value. We used three proxies for site quality of each plot: N-availability index as reported in McCarthy et al. (2010), pine basal area (B_{P96}), and pine leaf area index (L_{P96}); the latter two estimated in 1996, the year the CO_2 enrichment began in the replicated FACE.

2.3 | Statistical analyses

We tested CO_2 effects on NPP and *L* using data from 1997 to 2010 (excluding 2002–2003 affected by a combination of severe drought and an ice storm) collected in plots without N-additions. We used data from 2005 to 2010 to test the $CO_2 \times$ N-additions effects on the response variables. The experimental design was a randomized complete block with a split-plot where eCO_2 and N-additions were the main and split-plot effects, respectively. Treatment effects on NPP (by species group and organ) were tested using mixed effects models in *nlme*, *lme4*, and *lmerTest* packages in R (R Core Team, 2021). Block and block-by-CO_2 were treated as random variables (groups) with plots blocked according to the pairing of plots established at beginning of the experiment ($n = 4$). We evaluated the role of *L* in mediating the NPP responses by testing treatment effects on *L*, on NPP without *L* in the model, and on NPP with *L* included as an explanatory variable (covariate). In the most complete models for the NPP response, we included time (year), *L*, and volumetric soil moisture as continuous variables. When testing treatment effects on *L* we included B_{P96} as a covariate to account for variation in pre-treatment productivity. In addition, we analyzed treatment differences in ANPP-to-*L* relationships annually using analysis of covariance. We used linear regressions to evaluate trends in average enhancement ratios. We used a *t*-test to evaluate among-treatment differences in temporally averaged allocation ratios.

We used Shapiro–Wilk tests and Quantile–Quantile plots (R Core Team, 2021) to test for normality of each measured response variable, and data were transformed before model fitting when appropriate and back transformed as needed (Jørgensen & Pedersen, 1998). To evaluate temporal autocorrelation in time series of response variables (repeated measurements), we first fitted models with an autocorrelation function (acf; *nlme* package). We also fitted *nlme* models with and without a first-order autoregressive covariance structure (AR(1)). Based on the acf analyses and AIC fit statistics (comparing models with and without AR(1)), we found that temporal autocorrelation in all of the response variables was too small to justify using a more complex model and would not change the overall conclusions. Therefore, we fitted linear mixed models using the *lme4* package and reported the test results in analysis of variance tables (ANOVA, type III, *lmerTest* with Satterthwaite approximation for degrees of freedom). Significant treatment or interaction effects were

further analyzed using multiple comparisons with Tukey's test using *emmeans* package (R Core Team, 2021). Adjusted SEs of the models were calculated with the interactionMeans function in the package *phia* (De Rosario-Marinez, 2015).

3 | RESULTS

Aboveground net primary production (ANPP), NPP, and leaf area index (*L*) increased for the first 5 years of the study period as canopy volume was filling up and, again, after two major disturbances in 2002, a severe drought and an ice storm (Figure 2; NPP estimates by organ are shown in Figure S1). After the plots were split and nitrogen (N) additions commenced in 2005, and until the treatments ended in 2010 (marked by a vertical grey line), pine ANPP under ambient CO_2 (aCO_2) increased by 15% and pine *L* (L_P) by 11% ($p \le .060$). Expressed as an enhancement ratio over the same period, L_P enhancement under elevated CO_2 (eCO_2) declined by 8%–9% regardless of N-additions ($p \le .070$; Figures S2 and S3). After the treatments ended and half of the biomass was harvested in early 2011, estimates of pine ANPP, NPP and *L* decreased for 1 year and then recovered in the second year, likely in response to an increase in growing space and light availability for the remaining trees.

3.1 | Spatial variation in native site quality and NPP enhancement under elevated [CO_2]

Of our hypotheses (tests summarized in Figure 3), the first (H1) stated that the variation in the response of NPP to eCO_2 will reflect spatial variation in native site quality. We found that the absolute response of mean annual woody NPP (NPP_W) to eCO_2 increased with all three measures of site quality; N-availability index, initial pine basal area (B_{P96}), and pine leaf area index (L_{P96}; $p \le .016$ for $CO_2 \times L_{P96}$; Figure S4). While this interaction produced an increasing enhancement ratio (i.e., the ratio of the lines shown in Figure 3a) with site quality, the relationship was driven by one plot. Indeed, the mean plot-specific annual enhancement ratio (data points in Figure 3a; averaged over annual estimates of actual NPP_W under eCO_2 divided by the *expected value* at the same *L* but under aCO_2) was unrelated to L_{P96} ($p = .469$) and the other site quality proxies (not shown; $p \ge .173$).

Progressive N limitation (PNL) would result in a decline in the plot-specific enhancement ratio of NPP over time, which we expected to be most noticeable in plots with low L_{P96} (H2). While the enhancement ratio of NPP_W in each plot varied from year to year, contrary to our expectation, none showed a decreasing ratio (Figure 3b, $p \ge .387$). Note that, in these analyses, we used NPP_W, the production estimate with the longest record available from all plots. The fraction of NPP_W of total NPP (average ± SE over 1997–2010) was 78 ± 1.0% under eCO_2 and 76 ± 0.9% under aCO_2 ($p = .072$).

3.2 | Overall treatment effects on NPP

Over 1997–2010, pine ANPP was, on average, 35% ($p = .005$; ranging from 26% to 54% across years) and stand ANPP 33% higher ($p = .007$; 25%–48%) under eCO_2 compared to aCO_2 (% changes are based on unadjusted treatment means; *p*-values are taken from Table S1). Broadleaved ANPP was similar under both CO_2 treatments ($p = .446$). Enhancement of NPP for pine was of similar magnitude to that in ANPP (38%; $p = .004$; 28%–54%) but larger for broadleaved species (52%; $p = .051$; 37%–68%), reflecting a large coarse-root response. In both species groups, there was also a several-fold enhancement in reproductive NPP but, because the production of reproductive organs was at least an order of magnitude smaller than NPP of any other component (Figure S1 and Figure S3), the effect on total NPP was small. Because of the dominance of pine, stand NPP was 38% higher under eCO_2 ($p = .003$; 30%–53%).

Pine *L* was 19% ($p = .005$; 9%–20%) and stand *L* (L_T) 18% ($p < .026$; 7%–38%) higher under eCO_2, while broadleaved *L* (L_B) was similar under eCO_2 and aCO_2 ($p = .199$; −38%–103%; Table S2). Compared to aCO_2, production efficiency (PE = NPP/*L*) was 12% ($p = .014$; −2%–21%) and 46% ($p = .014$; 22%–77%) higher under eCO_2 for pine and broadleaved species, respectively. Interannual variation (1997–2010) in ANPP, NPP, and PE were unrelated to growing-season-averaged volumetric soil moisture (θ, precipitation or atmospheric vapor pressure deficit; $p \ge .110$). Although L_P appeared to decrease with θ ($p = .067$), the residuals (of a model without θ) were unrelated to θ (not shown).

The effect of N-additions (in 2005–2010) on pine ANPP and NPP were similar under both CO_2 treatments (Figure 4a–d; Table S3; based on models without *L*) demonstrating no CO_2xN interaction. While N-additions increased pine *L* only under aCO_2 (Figure 4e,f; Table 1), the treatment induced an additional increase in PE of both species groups under eCO_2 (Figure 4g,h, Table 2; based on models with *L*). In this shorter timeseries, L_P appeared to be lower in years with growing-season $\theta < 0.2\ m^3\ m^{-3}$ (Figure S5; Table 1). With L_P included in the model, θ appeared to have no direct effect on pine NPP ($p = .115$; Table 2). The effect of θ on both L_B and broadleaved NPP was statistically significant ($p \le .029$; Tables 1 and 2), however, the trend in L_B with θ was slightly negative and that in NPP slightly positive (not shown), making the soil moisture effect difficult to interpret.

In sum, the eCO_2-induced enhancement of pine ANPP and NPP and broadleaved NPP were sustained throughout the experiment, reflecting increases in pine *L* and in PE of both species groups, consistent with our expectations (H4). Moreover, PE was further enhanced by N-additions under eCO_2. While the enhancement of *L*, ANPP, and NPP varied widely across plots (Figure 5), based on treatment averages (2005–2010), the relative contribution to NPP of higher PE under eCO_2 and the two N treatments, was 38%–52% for pine and 67%–95% for broadleaved species (Figure 5e).

We also expected PE to decrease with increasing tree size, *L*, and within-canopy shading. We found that that PE declined with increasing *L* in broadleaved species but not in pine (Figure 3c,d).

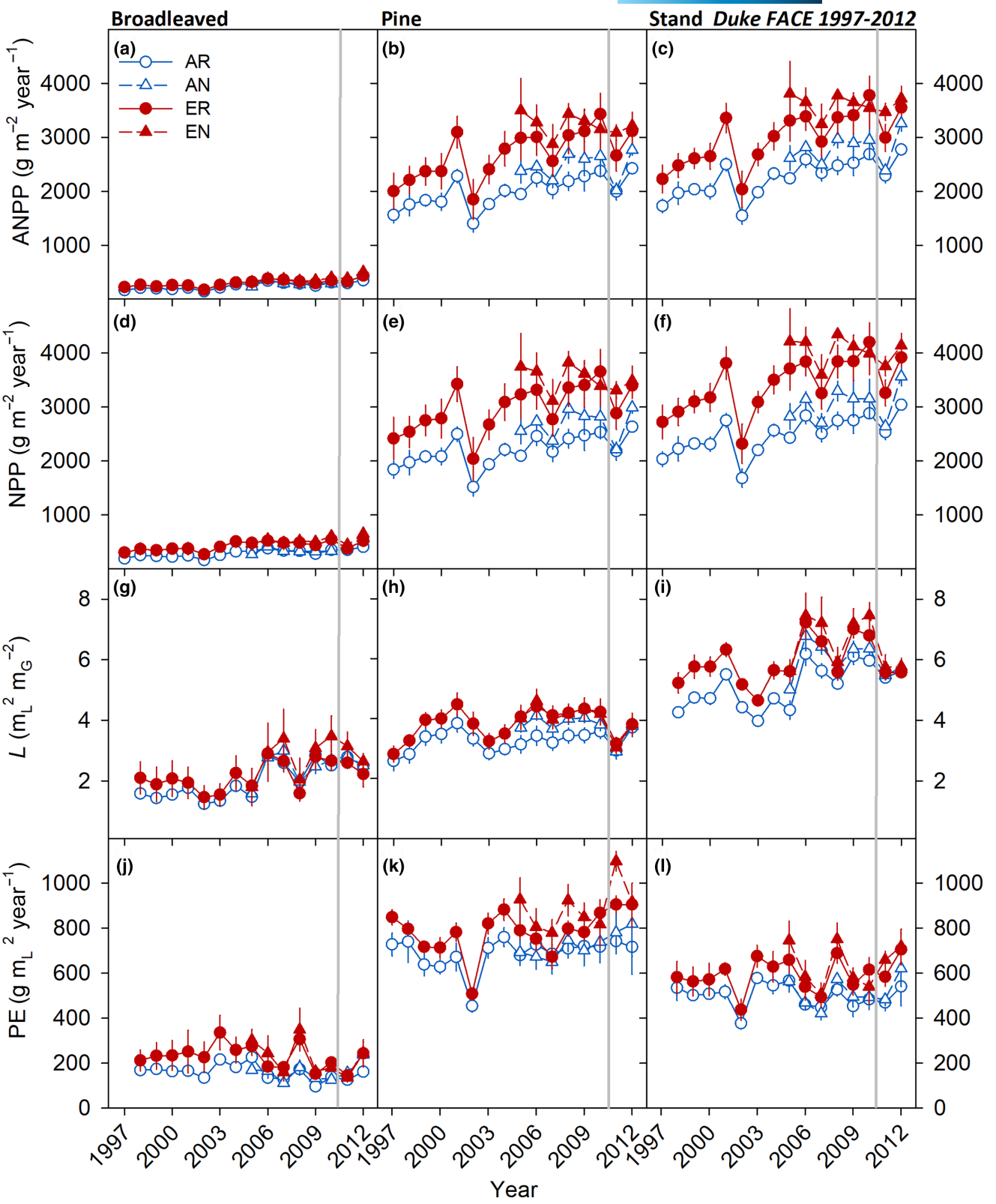

FIGURE 2 Temporal variation in treatment averages ($n = 3$–4) of aboveground net primary production (ANPP; a–c), NPP (d–f), leaf area index (L; g–i), and production efficiency (PE = NPP/L; j–l) for broadleaved species (left panels), pine (middle panels), and the stand (right panels). Error bars indicate SE (among plots). Ambient [CO_2] = AR, ambient [CO_2] with nitrogen-additions = AN, elevated [CO_2] = ER, and elevated [CO_2] with nitrogen-additions = EN. Vertical lines indicate the time of termination of treatments.

While L fluctuated, tree size and live biomass (M) increased monotonically over time. By the end of the experiment, trees in both species groups had grown larger under eCO_2 than those under aCO_2 (Figure 6). Relative growth rate (RGR) decreased with increasing M and, within the overlapping range of M, RGR was higher under eCO_2 ($p < .001$). Leaf area ratio (LAR) also decreased with increasing tree

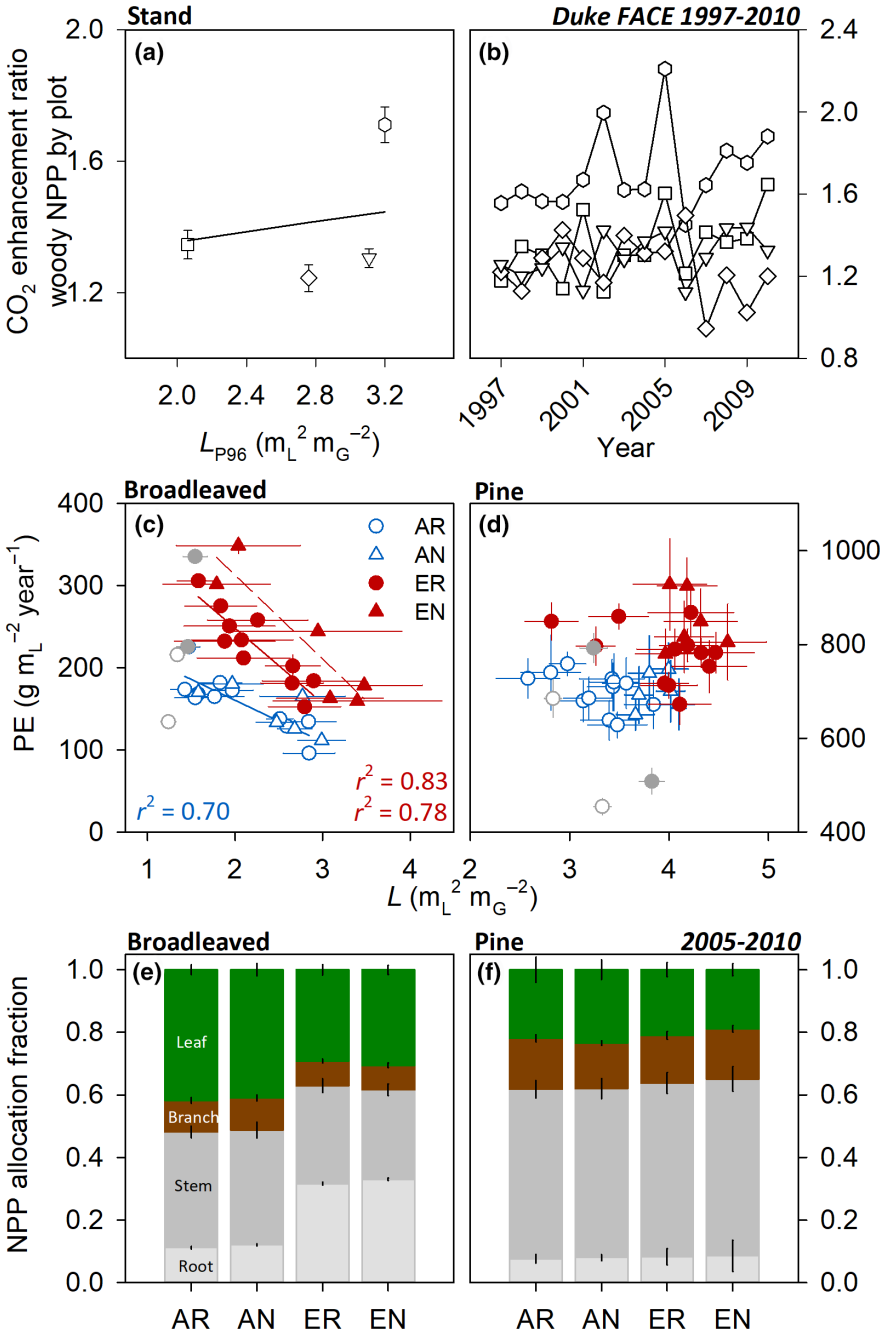

FIGURE 3 Enhancement of net primary production (NPP) of woody biomass under elevated atmospheric [CO_2] relative to that under ambient [CO_2] as a function of pine leaf area index in 1996 (L_{P96}; a). Variation in plot-specific CO_2-enhancement ratio over time (b). In (a), each point represents a mean plot-specific enhancement ratio estimated for plots without nitrogen-additions (estimated at a standard L) and averaged over 1997–2010. Error bars indicate SE (among years). Line represents the ratio between predicted NPP enhancement computed from CO_2-treatment-specific regression lines (see Figure S4). Annual mean production efficiency (PE = NPP/L), by treatment, for broadleaved species (c) and pine (d) as a function of their respective L. In (c, d), error bars indicate SE (among plots), and grey symbols represent data from 2002 to 2003 when L and production estimates reflect carryover effects from disturbances (see McCarthy et al., 2006, 2010). Treatment means for allocation fractions of NPP among root (coarse + fine), stem, branch, and leaf production (reproduction too small to show) for broadleaved species (e) and pine (f). In (e, f), each bar represents a mean over 2005–2010 and error bars indicate SE (among years). Ambient [CO_2] = AR, ambient [CO_2] with nitrogen-additions = AN, elevated [CO_2] = ER, and elevated [CO_2] with nitrogen-additions = EN.

size in both species groups. For pine, and at comparable M, LAR was higher under eCO_2 ($p < .001$). Except for broadleaved species under aCO_2, unit leaf rate (ULR = $\Delta M/L$), did not change with M and was, on average, higher under eCO_2 ($p < .001$).

3.3 | ANPP-to-L relationships over time

To demonstrate the dynamics in the relative roles of native site quality, eCO_2, N-additions and competition for light in driving production, we explored temporal changes in L_P relative to B_{P96}, variation in L_B relative to L_P, and in ANPP relative L. We focused on ANPP because broadleaved coarse-root NPP was not correlated with L_B (Table 2) and variation in NPP with L_B was less well-defined than that of ANPP.

At the beginning of the experiment, plots that showed larger B_{P96} also carried a higher L_P (Figure 7a–c and Figure S6). From 1999 onwards, at any given B_{P96}, eCO_2 plots showed a higher L_P than those under aCO_2, by a similar amount and regardless of N-additions. The differences among treatments disappeared after the CO_2 enrichment ended (Figure 7d). Broadleaved L, in turn, decreased with increasing L_P across plots (Figure 8a–c and Figure S7), indicating that the variation in L_B was driven by light availability. Within the common range in L_P, eCO_2 plots had a higher L_B than those under aCO_2. This difference appeared to diminish at higher L_P and disappeared altogether during the post-treatment years (Figure 8d).

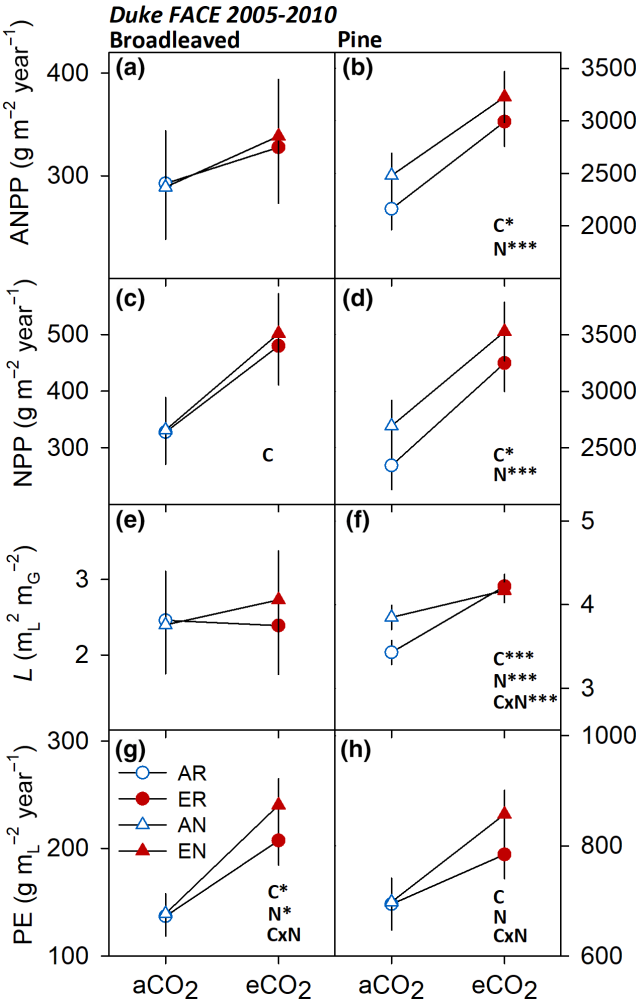

FIGURE 4 Atmospheric [CO_2] (ambient = aCO_2 and elevated = eCO_2) and nitrogen-addition (N) effects (2005–2010) on aboveground net primary production (ANPP; a, b), NPP (c, d), leaf are index (*L*; e, f) and production efficiency (PE = NPP/*L*; g, h) for broadleaved species (left panels) and pine (right panels). Each point represents an adjusted mean ($n = 4$) and error bars indicate adjusted SE. For a–d, the ANOVA results can be found in Table S3, and for e–h, in Tables 1 and 2; *** stand for $p < .001$, * for $p < .05$, and letter only for $p < .1$. Ambient [CO_2] = AR, ambient [CO_2] with nitrogen-additions = AN, elevated [CO_2] = ER, and elevated [CO_2] with nitrogen-additions = EN.

Earlier in the study, the response of pine ANPP to eCO_2 appeared to be greater in plots supporting high L_P but pine ANPP was similar under aCO_2 and eCO_2 in plots of low L_P (Figure 7e,f and Figure S8). This is consistent with the mean response over the entire period evaluated at fixed, initial L_P (L_{P96}; Figure S4). Towards the end of the experiment, and with both ANPP and L_P changing over time, plots across all treatments shared a common ANPP-to-L_P relationship (Figure 7g). For broadleaved species, spatial variation in L_B explained much of the variation in ANPP (Figure 8e–g and Figure S9). After the treatments ended, the ANPP-to-L_B relationship did not change much (Figure 8h). For pine, ANPP remained higher in the previously CO_2-fumigated plots compared to the ambient ones, but only at the upper end of the post-enrichment L_P (Figure 7h).

TABLE 1 ANOVA type III *p*-values related to linear mixed model fits (using the *lmer*Test package in R) for atmospheric [CO_2] (CO_2) and nitrogen-addition (N) effects on leaf area index of broadleaved species (L_B), pine (L_P), and the stand (L_T) over 2005–2010. Time (year), pine basal area in 1996 (B_{P96}), and growing season volumetric water content (θ) were included in the model as continuous variables.

Effect	L_B	L_P	L_T
CO_2	0.835	<0.001	0.112
N	0.367	<0.001	0.022
Year	0.001	0.192	0.001
B_{P96}	0.122	<0.001	0.414
θ	0.009	0.002	0.155
$CO_2 \times N$	0.175	<0.001	0.611

3.4 | Variation in allocation ratios, biomass retention

Across all treatments, the largest proportion of pine NPP was allocated to stem (~50%) while the fraction allocated to coarse roots declined with increasing *M* over time (Figure S10). At the beginning of the experiment, the largest fraction of broadleaved NPP was allocated to foliage and, by the end, allocation to foliage and stem was similar under aCO_2, and to foliage, stem, and coarse roots under eCO_2. Allocation ratios averaged over the last 6 years of the experiment demonstrate that, except for the increase under eCO_2 in broadleaved coarse-root NPP ($p < .001$) at the expense of leaves and stem ($p \le .038$), the rest of the ratios were within a few percentage points from each other across all treatments ($p \ge .091$; Figure 3e,f). Thus, in contrast to our expectations (H5), there was no reduction in the fraction of NPP allocated to roots (fine + coarse) due to N-additions in either species group ($p \ge .379$).

Finally, we compared the two production estimates, NPP (annual growth of living trees only) and ΔM (annual change in standing biomass; Figure 6). The overall slope of the relationship between ΔM and NPP was 0.78, whereas the mean ΔM-to-NPP ratio (averaged over the eight points in Figure 9b) was 0.57 under aCO_2 and 0.63 under eCO_2 ($p = .026$), indicating that a higher proportion of NPP was accumulating in living biomass under eCO_2.

4 | DISCUSSION

4.1 | The hypotheses

At this site, the initial leaf area index (*L*) was a good indicator of site quality, explaining most of the variation in biomass accumulation during the first decade of stand development (McCarthy et al., 2007, 2010). Accordingly, we hypothesized that eCO_2 will increase production more in plots with higher nutrient availability, as reflected in higher initial *L* (H1). We found that the *absolute* woody NPP (NPP_W) response to eCO_2 depended on all three indices of site

TABLE 2 ANOVA type III *p*-values related to linear mixed model fits (using the *lmer*Test package in R) for atmospheric [CO_2] (CO_2) and nitrogen-addition (N) effects on aboveground and total net primary production (ANPP, NPP) by biomass compartment and species group over 2005–2010; PE stands for production efficiency (NPP/leaf area index). Time (year), leaf area index for each species group (L_B, L_P and L_T), and growing season volumetric water content (θ) were included in the model as continuous variables.

Group	Effect	Reprod	Foliage	Branch	Stem	Root	ANPP	NPP	PE
Broadleaved	CO_2	0.994	0.264	0.641	0.471	0.001	0.466	0.041	0.013
	N	0.267	0.234	0.742	0.319	0.328	0.642	0.872	0.041
	Year	0.057	<0.001	0.556	0.856	0.435	0.038	0.262	0.024
	L_B	<0.001	<0.001	<0.001	<0.001	0.627	<0.001	<0.001	<0.001
	θ	0.017	0.007	<0.001	0.689	0.036	0.049	0.029	0.003
	$CO_2 \times N$	0.228	0.291	0.831	0.540	0.921	0.857	0.877	0.083
Pine	CO_2	0.001	0.751	0.006	0.104	0.121	0.059	0.063	0.075
	N	0.008	0.646	0.251	0.231	0.012	0.111	0.077	0.063
	Year	<0.001	0.008	0.036	0.157	<0.001	0.158	0.290	0.352
	L_P	0.005	<0.001	0.010	0.001	<0.001	<0.001	<0.001	0.573
	θ	0.505	0.133	0.003	0.092	<0.001	0.523	0.115	0.091
	$CO_2 \times N$	0.848	0.090	0.005	0.177	0.017	0.180	0.132	0.099
Stand	CO_2	<0.001	0.025	0.005	0.012	<0.001	0.008	0.005	
	N	0.005	0.014	0.064	0.023	<0.001	0.004	0.002	
	Year	<0.001	0.001	0.078	0.176	0.029	0.323	0.468	
	L_T	0.053	0.027	0.176	0.212	0.001	0.072	0.042	
	θ	0.137	0.370	0.145	0.011	<0.001	0.040	0.002	
	$CO_2 \times N$	0.627	0.001	0.042	0.863	0.766	0.630	0.633	

quality [N-availability index, initial pine basal area measured in 1996 (B_{P96}), and initial pine L (L_{P96}); Figure S4], consistent with earlier results (Finzi et al., 2002; McCarthy et al., 2010). The *enhancement ratio* computed based on the $CO_2 \times L_{P96}$ interaction effect on NPP_W increased slightly with L_{P96} (line in Figure 3a). However, based on an assessment of mean plot-specific enhancement ratios, an approach that reduces the effect of the fastest growing plot (with the greatest eCO_2 enhancement) on the relationships, the enhancement of NPP_W was unrelated to L_{P96} (data points in Figure 3a). Notably, two eCO_2 plots, especially the most responsive one, sustained their response following termination of enrichment even after their L decreased (Figure 7). This could be a legacy effect of eCO_2 (that was not found in L nor C allocation belowground; Kim et al., 2017); a structural adjustment over the long-term CO_2 enrichment that had a carryover effect on stand function, perhaps related to hydraulic adjustments (Domec et al., 2009).

We further hypothesized that the effect of eCO_2 on production will be ephemeral in plots of low L_{P96}, suggesting PNL (H2). We found little evidence of PNL, confirming the findings from earlier studies (Drake et al., 2011; Finzi et al., 2006, 2007; Kim et al., 2020; Maier et al., 2022; McCarthy et al., 2010). We evaluated the dynamics of NPP_W enhancement across the eCO_2 plots and over the entire study period and found no temporal trends (Figure 3b), thus leaving no basis for the hypothesis that N-addition will reverse PNL (H3). In other words, a sustained increase in production (shifting from line 1 to line 3 or 4 in Figure 1) was observed over the duration of the study. This contradicts an earlier observation at the FACE Prototype ($FACE_P$; one of two eCO_2 plots on poorer soil) that eCO_2 response of woody biomass production is ephemeral without complete nutrient addition (Oren et al., 2001); indeed, the response to eCO_2 recovered later and was sustained until the end of the study. The early attenuation of the growth response may have been a part of interannual variation triggered by that in climatic variables, yet no clear link was found. Alternatively, enhanced carbon allocation belowground (Drake et al., 2011; Maier et al., 2022; Palmroth et al., 2006), may have led to a release from nutrient limitation (Finzi et al., 2007; Walker et al., 2015) allowing a recovery of the response.

We found that increased pine NPP under eCO_2 was related to both increased L_P and PE (H4). Pine PE and unit leaf rate (ULR) did not decrease with increasing L_P and the associated within-canopy shading (Figures 3d and 6h), however, the expected inverse relationships were observed for the broadleaved component (only under $aCO_2$for URL; Figures 3c and 6g). The results also suggested that eCO_2 may have sustained the PE of the lower canopy strata under increasing shading by pine. Because PE includes all biomass production, a sustained efficiency suggests a higher canopy photosynthesis or carbon use-efficiency with increasing L. Although similar to full fertilization studies, where increased L was not accompanied by decreasing (growth) efficiency, in these experiments, growth efficiency is often based on stem production, which is sustained in part by reallocating less carbon (C) to belowground (Albaugh et al., 1998; Waring, 1983). In this study, both the absolute NPP of, and relative allocation to, broadleaved coarse roots increased under eCO_2, while pine above- and belowground NPP were similarly affected. Nitrogen-additions,

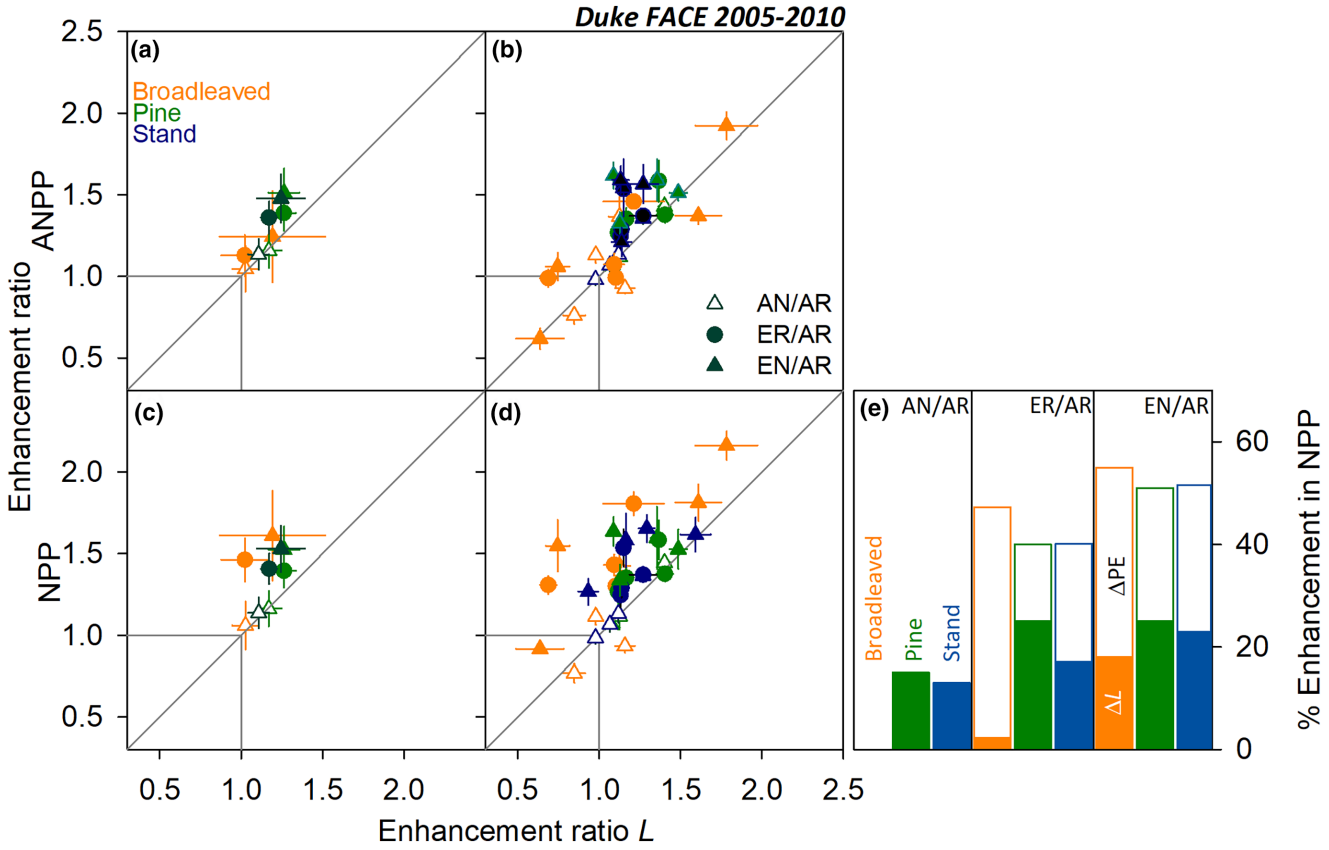

FIGURE 5 Enhancement ratio of aboveground net primary production (ANPP; a, b) and NPP (c, d) as a function of that of leaf area index (*L*) averaged for each treatment (a, c) and for each plot (four plots per treatment; b, d). Each point represents a mean ratio (over 2005–2010) and error bars indicate SE (among years or plots). Overall mean enhancement (2005–2010; e), where the solid section of bar represents leaf area-mediated enhancement (Δ*L*), and the open section shows the portion explained by production efficiency (ΔPE). Ambient [CO_2] = AR, ambient [CO_2] with nitrogen-additions = AN, elevated [CO_2] = ER, and elevated [CO_2] with nitrogen-additions = EN.

in turn, reduced fine-root production by 13% (Jackson et al., 2009), yet the fraction of NPP allocated to root production (coarse + fine) did not change with N-additions in either species group or CO_2 treatment, refuting H5 (Figure 3e,f).

4.2 | Sustained NPP enhancement under eCO_2 and its structural and functional drivers

The experimentally generated atmospheric [CO_2] (+200 μL L^{-1} under eCO_2) was 55% higher than ambient [CO_2] (aCO_2) in 1996, decreasing to 52% in 2005, and 51% at the end of the study. Accounting for site quality (as in Figure 3a) produced an estimate of eCO_2-induced enhancement of NPP_W of 40%, while the corresponding estimate based on the original block design was 38%. Averaged over the entire study period, the NPP of pine was enhanced by 38% and that of broadleaved species by 52% (Figure 2). Over the last 6 years of the experiment, these enhancements were estimated as 40% and 47% (Figure 5). Stand NPP estimates were comparable to those of pine as broadleaved NPP contributed only 10%–13% of the total production (Figure 10). Previous research demonstrated a limited NPP response to eCO_2 in the low N availability plots (Finzi et al., 2002; McCarthy et al., 2010), thus setting expectations that N-additions would induce a greater eCO_2 response. The increase in NPP under eCO_2 with N-additions was, however, relatively small and statistically significant only for pine (11% and 8% for pine and broadleaved species, respectively; Figure 5e). For pine, the increase in NPP under eCO_2 was similar above- and belowground, whereas the more than 200% increase in coarse-root NPP (Maier et al., 2022) made up the entire NPP response of broadleaved species.

We analyzed the production response using two approaches, one focusing on the components related to annual change in live biomass (Δ*M*; reflecting the balance between growth and tree mortality), the other on the *L* and PE components of NPP estimated for trees alive at the beginning and the end of a growing season. At comparable *M*, the RGR of both species groups was higher under eCO_2 than aCO_2 owing to higher unit leaf rate (ULR = Δ*M*/*L*) and, for pine, also higher leaf area ratio (LAR = *L*/*M*; Figure 6). Similarly, we demonstrated that NPP was higher under eCO_2 due to both greater PE (PE = NPP/*L*) and *L* (Figure 5). Note that our attempt to quantify the relative contributions of *L* and PE on NPP assumes that light interception increases linearly with *L* and, therefore, likely underestimates the role of PE. The assumption is, however, justified when the NPP-to-*L* relationship is close to linear, as in the current dataset

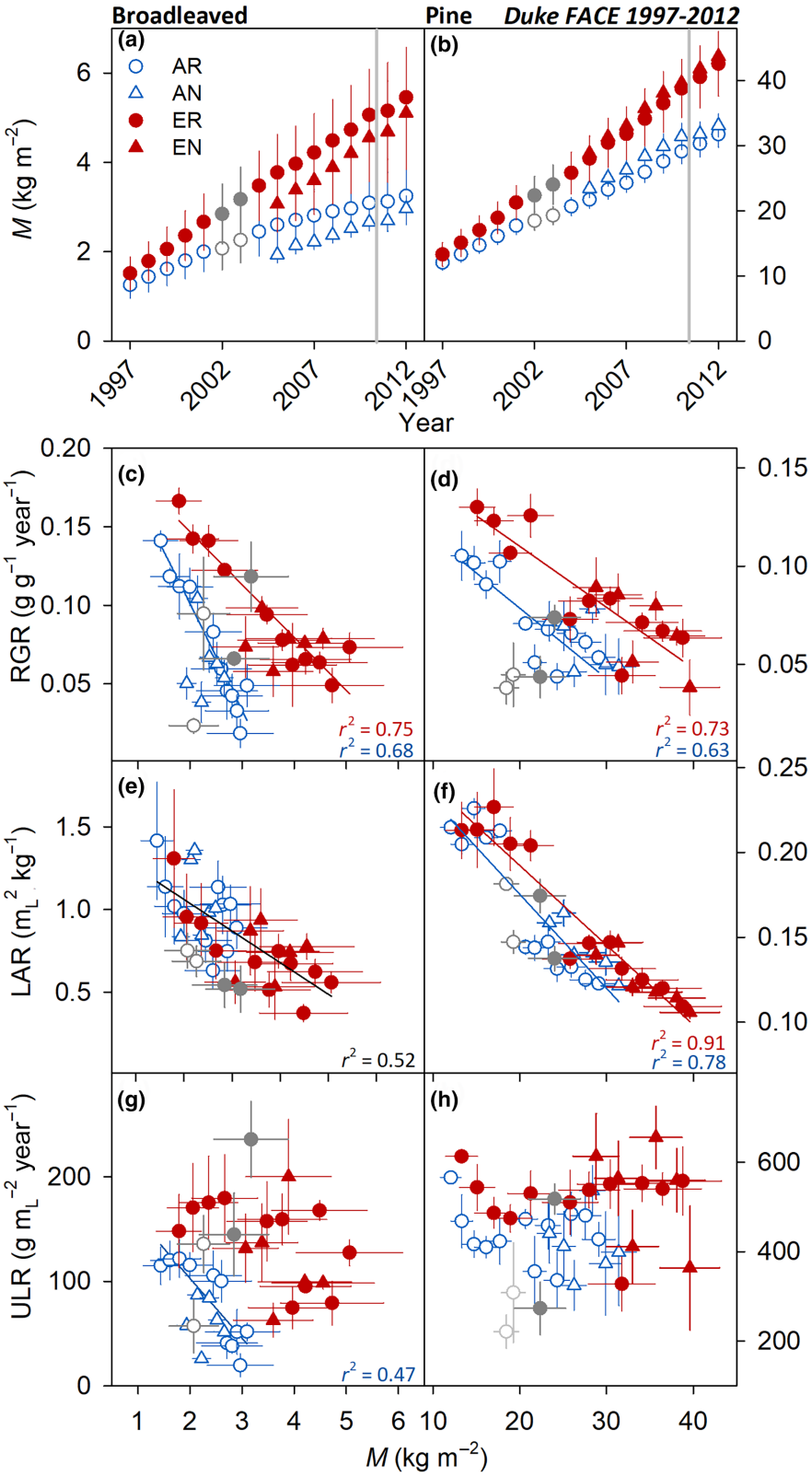

FIGURE 6 Total live biomass over time (*M*; a, b), and relative growth rate (RGR; c, d), leaf area ratio (LAR; e, f), and unit leaf rate (ULR = Δ*M*/*L*, where Δ*M* is annual change in *M* and *L* is leaf area index) as a funtion of *M* for broadleaved species (left panels) and pine (right panels). Each point represents a treatment mean ($n = 3–4$) and error bars indicate SE (among plots). Grey symbols represent data from 2002–2003 when *L* and production estimates reflect carryover effects from disturbances (see McCarthy et al., 2006, 2010). Vertical lines indicate the time of termination of treatments. Post-treatment years (2011–2012) are excluded from (c–h). Ambient [CO_2] = AR, ambient [CO_2] with nitrogen-additions = AN, elevated [CO_2] = ER, and elevated [CO_2] with nitrogen-additions = EN.

(Figures 7 and 8). Higher pine L_P under eCO_2 explained most of the increase in pine NPP, yet there was also a substantial functional response, particularly under eCO_2 with N-additions, where higher L_P and PE contributed nearly equally (Figure 5). While L_P responded to N-additions under aCO_2, the lack of response under eCO_2 suggests that L_P reached the maximum in each eCO_2 plot; lower maximum may reflect plot-scale limitation imposed by other resources.

If the CO_2-induced enhancement of growth under eCO_2 was primarily due to accelerated stand development, with no effect on maximum *L*, it would decline sometime after canopy closure, and the

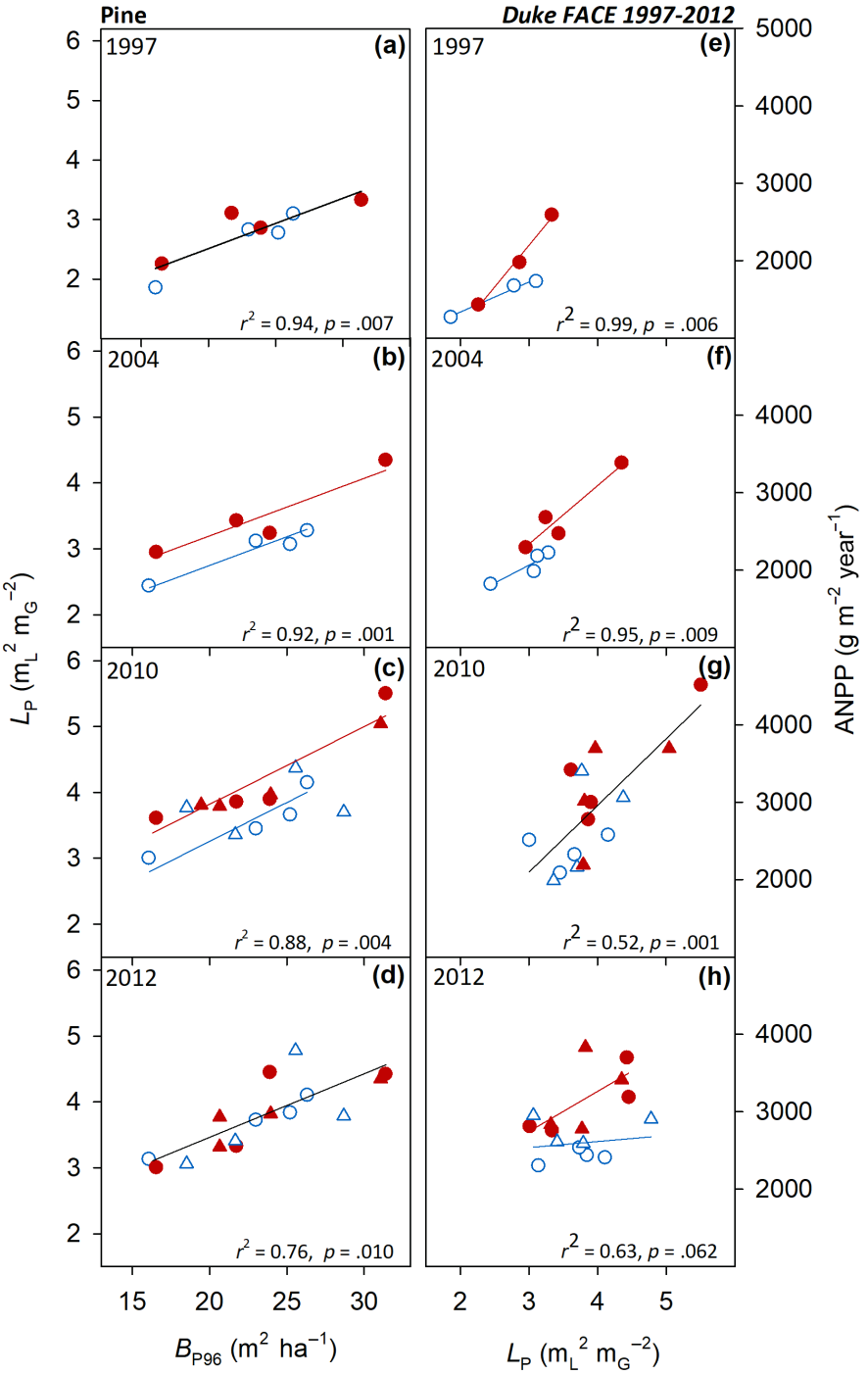

FIGURE 7 Pine leaf area index (L_P) as a function of pine basal area in 1996 (B_{P96}; a–d) and pine aboveground net primary production (ANPP) as a function of L_P (e–h) early in the course of the experiment (1997), a year before N-additions commenced (2004), the last year of treatments (2010), and 2 years after the termination of treatments (2012). Until 2005, each point represents a plot and a half-plot thereafter. Lines represent linear fits; two lines are shown if including CO_2 (a–d) or CO_2 and $CO_2 \times L_P$ (e–h) in the model significantly reduced the mean square error (*F*-test, $p \leq .095$). Ambient [CO_2] = AR, ambient [CO_2] with nitrogen-additions = AN, elevated [CO_2] = ER, and elevated [CO_2] with nitrogen-additions = EN.

difference in the steady-state *L* between the two CO_2 treatments would eventually disappear (Körner, 2006; Norby et al., 2022). Instead, we found a 19% higher L_P in eCO_2 plots and a decrease of the post-treatment L_P to that under aCO_2 (Figures 1 and 7, Figure S6; Kim et al., 2017). These results point to a direct CO_2 effect on maximum *L*, perhaps, as discussed above, due to the high CO_2 supply allowing leaves to maintain positive carbon balance under lower light availability (Long, 1991; Sprugel et al., 1991). Indeed, we observed higher RGRs under eCO_2 at a given size (biomass) and found no evidence for the rates of biomass increment slowing down faster under eCO_2 compared to aCO_2 (Figure 6; Kim et al., 2020).

Our results also show that the ratio between the annual change in live biomass (ΔM) and NPP was approximately 10% higher under eCO_2, following a relationship between ΔM:NPP and NPP that did not change by treatment (Figure 9), that is, higher NPP lead to higher ΔM:NPP. This increase in 'biomass retention' in live biomass could indicate a reduction in mortality or, as suggested in a recent analysis (Walker et al., 2019), an increase in C allocation to woody biomass. We found some indication for both changes. The fraction of NPP allocated to woody biomass increased by two percentage points to 78% under eCO_2, and cumulative tree mortality (since 1996; without N-additions) was lower under eCO_2 (17 ± 0.9%) than aCO_2 (23 ± 0.9%;

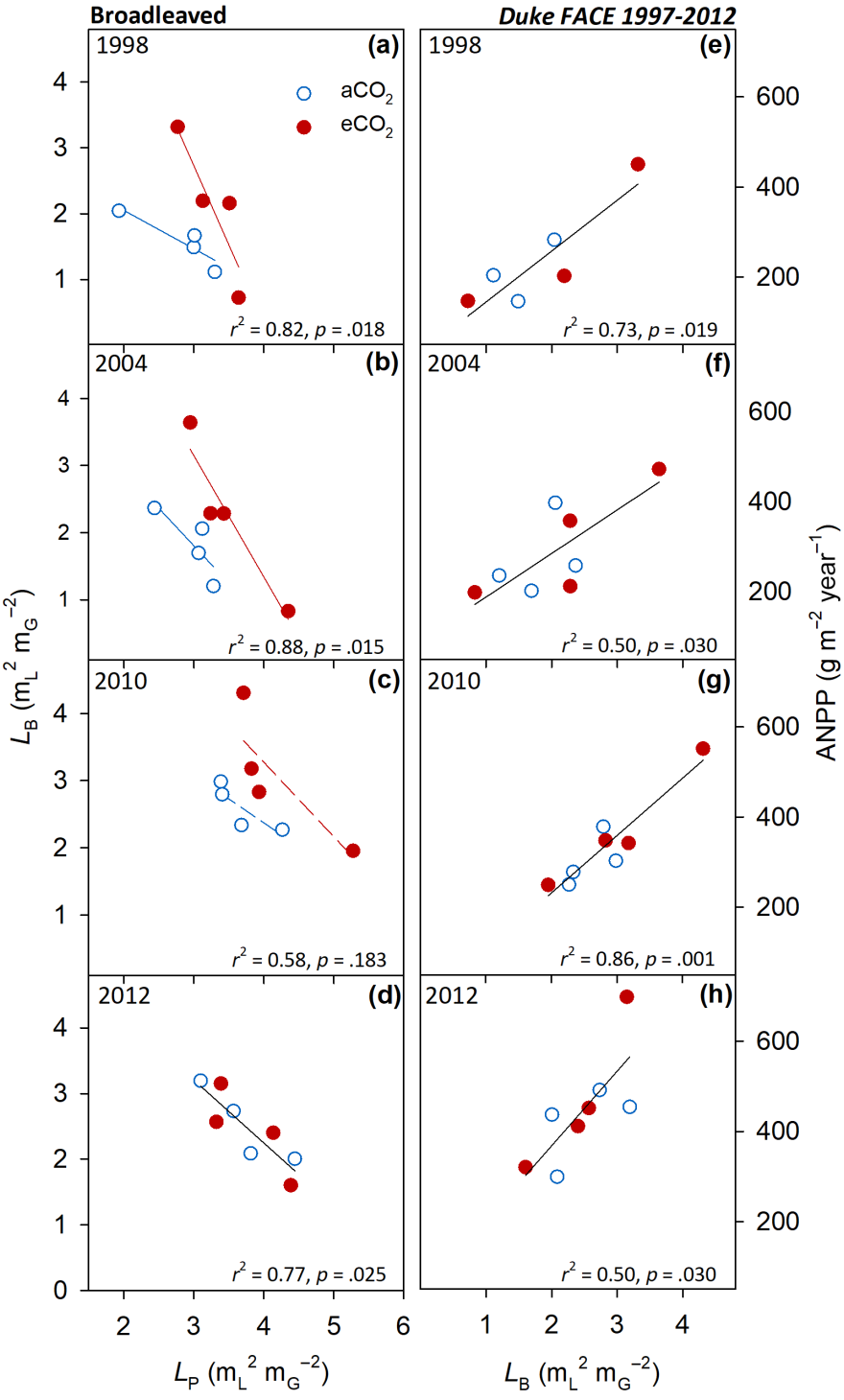

FIGURE 8 Broadleaved leaf area index (L_B) as a function of pine leaf area index (L_P; a–d) and broadleaved aboveground net primary production (ANPP) as a function of L_B (e–h) early in the course of the experiment (1998), a year before N-additions commenced (2004), the last year of treatments (2010), and 2 years after the termination of treatments (2012). For 2005–2012, each point represents a mean over plot-halfs with and without nitrogen-additions. Open symbols represent ambient atmospheric [CO_2] (aCO_2) and filled symbols elevated [CO_2] (eCO_2) conditions. Lines represent linear fits; two lines are shown if including CO_2 (a–d) or CO_2 and $CO_2 \times L_B$ (e–h) in the model significantly reduced the mean square error (F-test, $p \leq .098$).

$p = .013$). Moreover, the litterfall of shorter-longevity organs (leaves, branches, reproductive organs) did not increase in proportion with NPP under eCO_2 (Figure 10; $p = .344$ for eCO_2 effect on litterfall).

Consistent with earlier studies on understory L and aboveground biomass (Kim et al., 2016, 2020; McCarthy et al., 2010), we demonstrated that the lack of eCO_2 response in broadleaved L (L_B) and ANPP was likely due to light limitation. We showed that L_B decreased with increasing L_P across plots (Figure 8 and Figure S7) and, although L_B was somewhat higher under eCO_2 where L_P was low, the difference diminished with increasing L_P. Higher broadleaved NPP under eCO_2 was mostly explained by higher PE (Figures 4 and 5). The increase in PE implies not only higher carbon uptake per unit leaf area, perhaps due to sustained lower photorespiration and decreased photosynthetic light compensation point (Drake et al., 1997; Long, 1991; Springer & Thomas, 2007), but also increased sink strength belowground (Körner, 2006). The largest increase in the broadleaved coarse-root biomass and NPP was found in larger root classes (>15 mm) and deeper soil layers (30+ cm). While the reason for the large response remains unknown, Maier et al. (2022) suggested that competition with pine roots closer to the surface may have precluded a large growth

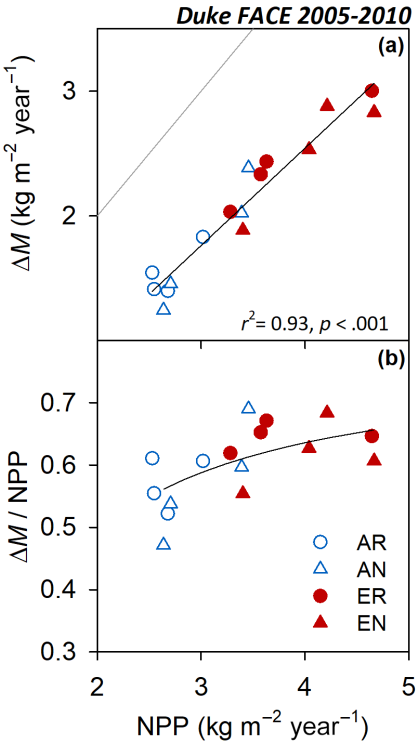

FIGURE 9 Annual change in live biomass (Δ*M*) by treatment, averaged over 2005–2010 (a) and the ratio between Δ*M* and net primary production (NPP; b) as a function of NPP. The black line in (b) is calculated using the slope and intercept in (a) and the grey line in (a) is 1:1 line. Ambient [CO_2] = AR, ambient [CO_2] with nitrogen-additions = AN, elevated [CO_2] = ER, and elevated [CO_2] with nitrogen-additions = EN.

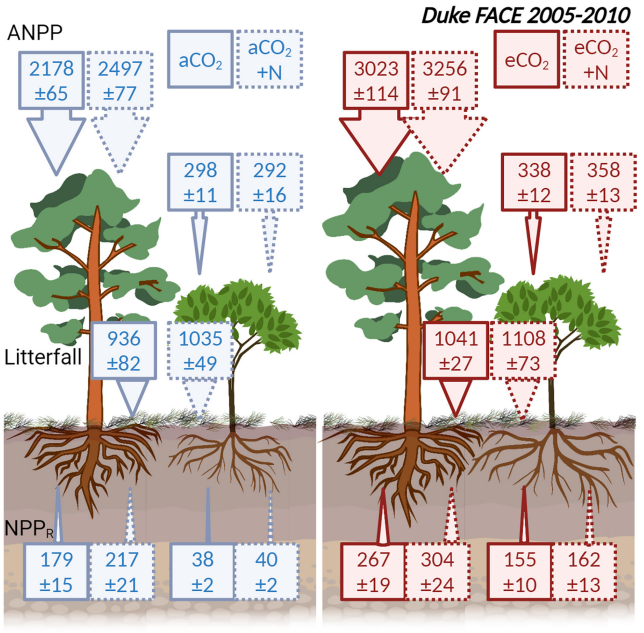

FIGURE 10 Time-averaged (2005–2010) aboveground net primary production (ANPP) of pine and broadleaved species, NPP of course roots (NPP_R) for each species group, and annual litterfall for the stand [all fluxes are in g m^{-2} $year^{-1}$ ± SE (among years)] under ambient [CO_2] = aCO_2, elevated [CO_2] = eCO_2, and nitrogen-additions = +N. Image: mariaflaya/Depositphotos.com, BioRender.

response there or made the investment of the extra carbohydrate produced under eCO_2 in deeper roots a more efficient strategy.

The sustained eCO_2 effect on NPP and its limited interaction response to N-additions, can be explained by a higher C partitioning belowground both in terms of root production allowing access to unexploited soil volume and access to nutrients in previously unavailable pools (Drake et al., 2011; Jackson et al., 2009; Maier et al., 2022; Pritchard et al., 2008). Drake et al. (2011) argued that higher carbon flux belowground (to mycorrhiza and as root exudates) under eCO_2 stimulated both soil organic matter decomposition and tree N uptake, where the role of mycorrhiza in boosting N uptake may be less important than the faster turnover of soil organic pools (Phillips et al., 2011; Pritchard et al., 2014). Although these processes are discussed in terms of N, it may not be the sole nutrient the limitation of which have been alleviated under eCO_2 by better exploitation of the soil and increased decomposition rate.

Southeastern US piedmont soils are often phosphorous (P) and potassium (K) deficient, and by the end of the study, the foliar P:N and K:N ratios estimated for these pines were low (Knier, 2022), far below optimum for loblolly pine (Albaugh et al., 2010). Results from Duke $FACE_P$ suggested co-limitation of several nutrients as growth enhancement under eCO_2 was greatly increased with balanced nutrient fertilization (Oren et al., 2001). Similarly, two studies on extremely poor fertility sites, one on *P. taeda* (sandy soil) and the other on *Picea abies* (sandy, post-glacial till), showed growth response to eCO_2 in large-tree chambers only under balanced fertilization (Oren et al., 2001; Sigurdsson et al., 2013). In other FACE experiments, absence of eCO_2-induced growth enhancement in a mature eucalyptus (*Eucalyptus tereticornis*) forest was attributed to low phosphorus availability (Ellsworth et al., 2017; Jiang et al., 2020), and low availability of P or other nutrients may have contributed to similar findings in a mature beech-oak (*Fagus sylvatica*, *Qercus petraea*; Bader et al., 2013) and Norway spruce (*Picea abies*) forests (Klein et al., 2016).

4.3 | New site-specific allometric functions, new NPP estimates for Duke FACE

Our estimate of 38% for the average enhancement of stand NPP under eCO_2 is higher than the median of 23% presented for young forests (Norby et al., 2005) and the 27% previously reported for Duke FACE (McCarthy et al., 2010). This was expected. By the end of the study, pines grown under eCO_2 were taller for a given diameter, and based on these site-specific allometric functions pine biomass was 27% higher than under aCO_2 compared to 21% estimated using generic equations (Kim et al., 2020). Consequently, NPP estimates were higher and the difference between the CO_2 treatments larger.

Our estimates also include, for the first time, branch turnover as the live crowns ascend over time (Valentine et al., 2013). This

oft-ignored production component represented ~18% of the current aboveground woody NPP estimates at Duke FACE. Moreover, our coarse root biomass and NPP estimates, based on root harvest at the end of the study (Maier et al., 2022), were also larger than reported by McCarthy et al. (2010). In fact, the current broadleaved coarse-root NPP estimates under eCO_2 were similar in magnitude to estimates of leaf and stem NPP and resulted in a mean enhancement ratio of 52% for broadleaved NPP, similar to that reported for another FACE experiment on *Populus tremuloides* (Norby et al., 2005). Like for *P. tremuloides*, in absolute terms, our broadleaved NPP estimates were low, making the enhancement ratio sensitive to errors in any of the components.

Our results, in context with earlier findings, indicate that NPP of this pine-dominated stand increased under eCO_2. Not only was higher PE sustained over the years of CO_2 enrichment, but also the amount of pine leaf area per biomass and L_P increased. This suggests that the shade-intolerant *P. taeda* behaved as if its self-shade tolerance increased (Zeide, 1987), which may indicate a higher steady-state biomass at the site. However, the stand was too young for us to evaluate whether the higher growth rate under eCO_2 would affect maximum tree age and C residence time (Brienen et al., 2020; Büntgen et al., 2019). We can only certainly say that the stand follows either curve 3 or 4 (Figure 1), based on processes shown in inset c, with some indication that it may not only sequester carbon faster under eCO_2, but end up with a greater carbon storage in live biomass. Such trajectories can be simulated by models that have been evaluated against observations, including treatment-specific self-thinning curves.

4.4 | Toward improved ecosystem models

The results presented here offer opportunities to evaluate and improve ecosystem models. Ecosystem models with reasonable reproduction of observed results can be used to extrapolate results beyond the timeframe of experiments. However, ecosystem models that simulate the responses of forests to eCO_2 can be complex, and it is not always clear why a given model simulates a particular value for forest biomass or NPP. To gain robust insight into model performance, processes subordinate to total biomass or NPP need to be evaluated (Medlyn et al., 2015). These subordinate processes may be component processes of the main process (e.g., light capture and PE are components of NPP), or specific to the level of plant organs and/or plant species. The component-process analysis and organ-level and species-level results in this study (e.g., Figures 2 and 10, and Figure S1) will enable the validation of models at that level. Our results also will enable validation of whether models simulate realistic functional responses and responses to varying initial conditions (Figures 7 and 8). Understanding model performance and biases at these scales enables the pinpointing of areas for model improvement and better understanding a model's projections of ecosystem responses to future CO_2 concentrations.

Earth system models (ESM) rely on estimated responses of terrestrial carbon sinks to increasing $[CO_2]$ for predictions of future atmospheric $[CO_2]$. Recent analyses showed that terrestrial ecosystem sinks are greatly underestimated when ESM predictions are compared to sink estimates from inversion of atmospheric CO_2 measurements, especially in North America and Europe (Byrne et al., 2023). Ample information is available for evaluating model estimates against current ecosystem sink strength. However, there is little information for judging how fit models are to predict future sink strength as atmospheric $[CO_2]$ increases. Our study, one of the very few obtained at the climate-change relevant spatiotemporal scale (ecosystem and 1.5 decades), demonstrates sustained sink enhancement due to increased leaf area, production efficiency, and carbon retention. These unique results will help further constrain model predictions.

AUTHOR CONTRIBUTIONS

S. Palmroth: Formal analysis; investigation; writing – original draft; writing – review and editing. **D. Kim:** Data curation; formal analysis; investigation; writing – review and editing. **C. A. Maier:** Investigation; writing – review and editing. **D. Medvigy:** Writing – review and editing. **A. P. Walker:** Writing – review and editing. **R. Oren:** Conceptualization; funding acquisition; investigation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the ESS-DIVE repository at https://data.ess-dive.lbl.gov/datasets/doi:10.15485/2283434.

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SUPPORTING INFORMATION

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