

Evapotranspiration and water yield of a pine-broadleaf forest are not altered by long-term atmospheric [CO₂] enrichment under native or enhanced soil fertility

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Abstract

Changes in evapotranspiration (*ET*) from terrestrial ecosystems affect their water yield (*WY*), with considerable ecological and economic consequences. Increases in surface runoff observed over the past century have been attributed to increasing atmospheric CO₂ concentrations resulting in reduced *ET* by terrestrial ecosystems. Here, we evaluate the water balance of a *Pinus taeda* (L.) forest with a broadleaf component that was exposed to atmospheric [CO₂] enrichment (ECO₂; +200 ppm) for over 17 years and fertilization for 6 years, monitored with hundreds of environmental and sap flux sensors on a half-hourly basis. These measurements were synthesized using a one-dimensional Richard's equation model to evaluate treatment differences in transpiration (*T*), evaporation (*E*), *ET*, and *WY*. We found that ECO₂

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did not create significant differences in stand T , ET , or WY under either native or enhanced soil fertility, despite a 20% and 13% increase in leaf area index, respectively. While T , ET , and WY responded to fertilization, this response was weak (<3% of mean annual precipitation). Likewise, while E responded to ECO_2 in the first 7 years of the study, this effect was of negligible magnitude (<1% mean annual precipitation). Given the global range of conifers similar to *P. taeda*, our results imply that recent observations of increased global streamflow cannot be attributed to decreases in ET across all ecosystems, demonstrating a great need for model–data synthesis activities to incorporate our current understanding of terrestrial vegetation in global water cycle models.

1 | INTRODUCTION

Evapotranspiration (ET) is the transfer of water from land to atmosphere through the combined processes of evaporation from plant and soil surfaces and transpiration through leaf stomata of water extracted from the rooting zone. The terrestrial imbalance between precipitation (P) and ET determines the ecosystem water yield (WY) in the form of runoff and drainage, which supports downstream ecosystems and recharges aquifers and reservoirs. Thus, changes in terrestrial ET and WY can have considerable ecological and economic consequences (Gedney et al., 2006; Katul, Oren, Manzoni, Higgins, & Parlange, 2012; Milly, Dunne, & Vecchia, 2005; Reay, Dentener, Smith, Grace, & Feely, 2008; Rind, Rosenzweig, & Goldberg, 1992). Increases in river flow observed over the past century have been attributed to increasing atmospheric CO_2 concentrations resulting in reduced ET by terrestrial ecosystems (Gedney et al., 2006; Matthews, 2006; Rigden & Salvucci, 2017). Further substantial increases in river flow are projected in many regions, based on results from general circulation models (Betts et al., 2007; Milly et al., 2005). Lower forest ET would increase WY and provide for downstream ecosystems and water users (Oishi, Oren, Novick, Palmroth, & Katul, 2010), but may also alter energy budgets and lead to increased surface temperature (Bonan, 2008; Cao, Bala, Caldeira, Nemani, & Ban-Weiss, 2010; Juang, Katul, Siqueira, Stoy, & Novick, 2007).

Responses of forests to increasing atmospheric CO_2 concentration are complex, depending not just on immediate responses to atmospheric CO_2 concentration, but also on structural and physiological changes in the ecosystem over time. Changes such as increasing leaf area index (L) (McCarthy et al., 2007; McCarthy, Oren, Finzi, & Johnsen, 2006), increasing rooting depth (Iversen, Keller, Garten, & Norby, 2012; Luo, Hui, & Zhang, 2006; Pritchard et al., 2008), and decreasing stomatal conductance (Bazzaz, 1990; Bunce, 1998; Drake, Gonzalez-Meler, & Long, 1997; Herrick, Maherali, & Thomas, 2004; Lockwood, 1999; Medlyn et al., 2001; Schäfer, Oren, Lai, & Katul, 2002; Warren, Pötzelsberger, et al., 2011) may affect ET , but the magnitude of these responses vary with edaphic characteristics of sites, such as soil nitrogen availability (McCarthy et al., 2007; Ward et al., 2013).

Resolving such complex interactions was the aim of many large-scale ecosystem manipulations of preceding decades, such as those conducted using free-air CO_2 enrichment (FACE) technology, and remains a goal for future manipulations (Hendrey & Kimball, 1994; Norby et al., 2016). The Duke Forest FACE Experiment was the first to use FACE technology in a mature forest (Hendrey, Ellsworth, Lewin, & Nagy, 1999). Long-term study of this temperate *Pinus taeda* L. (loblolly pine) plantation subjected to elevated atmospheric CO_2 concentrations (ECO_2) and nitrogen (N) fertilization has shown treatment differences likely to affect the hydrological budget. This FACE experiment was the only one in a conifer-dominated stand and provides the best basis for models of the future ecohydrological behavior of forests composed of similar species. For over 17 years, many components of the hydrologic cycle were measured to assess the effects of ECO_2 and N availability on forest hydrological budget. For the period 1998–2000, the hydrological budget of the experiment showed no effect of ECO_2 on evapotranspiration (ET), although the average soil moisture was reported as higher in ECO_2 plots (Schäfer et al., 2002). Earlier results from field-grown *P. taeda* at this and other sites concluded that stomatal conductance was insensitive to ECO_2 (Ellsworth, Oren, Huang, Phillips, & Hendrey, 1995; Pataki, Oren, & Tissue, 1998). It was therefore not particularly surprising that ET was also unaffected, given that L did not increase under ECO_2 (Schäfer et al., 2002).

Since 2000, subsequent studies have detected several tree and stand-scale changes under ECO_2 that could influence the hydrological budget and change this conclusion. First, there are interactions of soil fertility and ECO_2 resulting in variable enhancements of L relative to control plots as the experiment progressed (McCarthy et al., 2007). These increases in L may have contributed to increased ET through increased surface area for both interception and transpiration. However, decreased stomatal conductance of *P. taeda* under ECO_2 was also noted in later years (Ward et al., 2013), potentially related to increased mutual shading or decreased hydraulic supply of water to the canopy from changes in stand structure or in leaf xylem anatomy (Domec et al., 2009; Domec, Palmroth, & Oren, 2016). In addition, increased litter layer thickness driven by the

higher L (Finzi et al., 2007; Lichter et al., 2008; Schlesinger & Lichter, 2001) has potential implications for surface evaporation and runoff (Schäfer et al., 2002). Belowground, increased fine root biomass (Jackson, Cook, Pippen, & Palmer, 2009; Matamala & Schlesinger, 2000; Pritchard et al., 2008) could potentially increase ET by allowing better access to soil moisture (Ewers, Oren, & Sperry, 2000; Hacke et al., 2000). However, the addition of N reduced the amount of fine roots under both $[CO_2]$ conditions (Drake et al., 2011; Jackson et al., 2009), possibly counteracting this effect in fertilized plots. Further complicating the predicted treatment effects on ET was a decreased vulnerability in ECO_2 plots to damage from a major ice storm in December of 2002 (McCarthy, Oren, Kim, et al., 2006) that may have decoupled the interannual dynamics of hydrologic budget components of ECO_2 plots from ambient (ACO_2) plots. Given the number of physiological processes and hydrological budget components involved, and feedbacks among them, empirical data are essential to assess the response of ET to ECO_2 in different fertility regimes, and quantify the overall effect on the hydrologic cycle.

Here, we perform a comprehensive assessment of the water budget and all of its components over 13 years (1998–2010), including 6 years of N fertilization (2005–2010), against the backdrop of naturally varying climatic conditions at Duke FACE. We present an additional 4 years of transpiration data preceding the initiation of replicated treatments to extend the analysis of the prototype plot to 17 years. Data from this site have already been shown to be of crucial importance to understanding ECO_2 responses in data assimilation efforts to project pine forest productivity in the southeastern United States (Thomas et al., 2017), which could play a major role in regional carbon sequestration (Johnsen et al., 2001). However, given that the range of forests dominated by physiologically similar species extends from 35° S to 64° N (Tor-ngern et al., 2017), the impact is far from regional. This analysis is aimed at resolving ECO_2 effects on ET at this site, which is poorly predicted by many ecosystem models (De Kauwe et al., 2013).

It has been suggested that ET is a rather conserved value for forests in terms of both spatial variation within large regions (Roberts, 1983) and in terms of interannual variability at single sites (Ohta et al., 2008; Oishi et al., 2010; Wilson & Baldocchi, 2000). We concentrate on annual values of the hydrological budget components to determine whether ECO_2 , under native fertility or with N amendment, altered the balance in favor of WY at the expense of ET , as suggested for terrestrial ecosystems in general (Gedney et al., 2006), or if these two fluxes are generally conserved despite the myriad changes observed in their components under ECO_2 .

2 | MATERIALS AND METHODS

2.1 | Setting

The Duke FACE experiment was located in a loblolly pine (*Pinus taeda* L.) plantation established in 1983 in the Blackwood division of Duke Forest, North Carolina (35°58' N, 79°08' W, and elevation

163 m). The moderate fertility site, with slope of < 5%, has acidic clay-loam soil (Enon series), increasing in depth and fertility with slight changes in elevation (McCarthy et al., 2007). Summers are warm and humid, winters are moderate, and mean annual temperature is 15.5°C. The nearly evenly distributed precipitation (P) has a 111-year average of 1,145 mm. Common broadleaf species include sweetgum (*Liquidambar styraciflua* L.) and tulip poplar (*Liriodendron tulipifera* L.) in the mid-to-upper canopy; and red maple (*Acer rubrum* L.), winged elm (*Ulmus alata* Michx.), and flowering dogwood (*Cornus florida* L.) in the mid-to-lower canopy.

In 1993 an untreated 30 m diameter plot (plot 8) was established as a part of another study, followed in 1994 by the nearby FACE prototype plot of similar dimensions (plot 7). CO_2 enrichment (550 mmol/mol during daylight hours of the growing season) delivered by 32 vertical pipes surrounding the plot commenced in 1994 according to the FACE protocol (Hendrey et al., 1999). The infrastructure for the replicated FACE experiment (plots 1–6) was completed in 1996 and CO_2 enrichment (+200 mmol/mol above ambient) commenced in three of the plots in August of that year. Elevation in CO_2 was maintained as long as air temperature was $\geq 5^\circ C$ and wind speed < 5.0 m/s. Beginning in 2006, CO_2 enrichment was restricted to daytime only. Target CO_2 concentration was achieved in the inner 26 m diameter circle of the 30 m diameter plot, so all measurements and scaling were performed within this area.

In fall 1998, plots 7 and 8 were split in half using an impermeable barrier to a depth of 0.7 m, below the rooting zone and one half of each plot (including a 7.5 m buffer arcing outside the plot) received annual nitrogen addition in the form of urea pellets (11.2 g N m⁻² year⁻¹). In early spring of 2005, the same treatment was extended to the rest of the plots. Measurements of tree diameter at 1.35 m performed at, or interpolated to, weekly intervals were used together with allometric relationships relating sapwood thickness to diameter outside bark to estimate intra- and interannual dynamics of sapwood area per unit ground area for each species (McCarthy et al., 2007; McCarthy et al., 2010; Phillips & Oren, 2001; Schäfer et al., 2002). L was obtained from a combination of litter fall and optical measurements after McCarthy et al. (2007). Converting the volumetric measurements into amount of stored water required an estimate of rock content. Volumetric rock content was obtained from two pits (0.3 x 0.3 x 0.3 m) within each plot and two pits (0.5 x 0.5 x 0.3 m) directly adjacent the plots (Table 1; see McCarthy et al., 2010 for further details).

2.2 | Environmental variables

Air temperature (T_A) and relative humidity, used to calculate vapor pressure deficit (D), 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, Nebraska, USA) for measuring photosynthetically active radiation (PAR) and an automated system (tipping bucket TR-525USW; Texas Electronics, Dallas, Texas, USA) for measuring P were

TABLE 1 Soil properties used in hydrologic balance model, including saturated volumetric water content (θ_s , $\text{m}^3 \text{H}_2\text{O m}^{-3}$ soil), hygroscopic water content (θ_H , $\text{m}^3 \text{H}_2\text{O m}^{-3}$ soil), saturated water potential (Ψ_s , $\text{cm H}_2\text{O}$), the exponent of the water desorption curve (b), saturated hydraulic conductivity (K_s , cm/day), and the rock content (RC , %) of soil

Depths (m)	θ_s	θ_H	Ψ_s	b	K_s	RC
0–0.1	0.54	0.1	37.5	3.53	28.4	9.24
0.1–0.2	0.54	0.09	18	3.83	28.4	9.24
0.2–0.4	0.54	0.09	18	3.83	12	9.24
0.4–1.0	0.54	0.19	5.3	13.7	1.42	9.24

mounted. Net radiation measurements were made in an ambient CO_2 plot (Plot 1) with Fritschen-type net radiometers (Q7, REBS, Seattle, WA, USA) through 2003 and with CNR1 net radiometers (Kipp & Zonen, Delft, the Netherlands) thereafter. All sensors were sampled every 30 s, and 30-min averages were logged (CR21X or CR23X; Campbell Scientific, Logan, Utah, USA). Beginning in 1997, volumetric soil water (θ ; $\text{m}^3 \text{water m}^{-3}$ soil) of the upper 30 cm soil layer was measured continuously at four locations in each of plots 1–6 (CS615 or CS616; Campbell Scientific, Logan, Utah, USA); beginning 2001, volumetric soil water content was measured continuously in plots 7 and 8 at eight locations, with four probes measuring at 5–10 cm depth and four probes at 25–30 cm depth (ThetaProbe ML1x or ML2x; Delta-T Devices, Cambridge, UK). Soil moisture for each treatment was rescaled to measured porosity (representing saturated water content) and hygroscopic minimum (Table 1), after Oishi, Oren, and Stoy (2008).

2.3 | Sap flux measurements and transpiration

In each plot from 1998 to 2010, *P. taeda* and *L. styraciflua* were selected for sap flux measurements based on the Granier-type constant heat dissipation sensor (Granier, 1985, 1987). Temperature difference in each probe set was monitored every 30 s, and 30-min averages were stored on the same logger used for storage of environmental data. The signal was converted into sap flux density with zero-flux points conditional on nighttime values of D and signal stability (Oishi et al., 2008). The number of sensors increased as the experimental setup changed and as tree sapwood depth increased. By the end of the study, 240 sensors were continuously monitored, reaching a maximum depth of 60 mm from the cambium (Supporting Information Table S1).

Scaling of sap flux density to leaf area averaged transpiration and stomatal conductance for each species followed Ward et al. (2013), using the StaCC model (Bell et al., 2015) and extended the dataset to include 2009–2010. Deciduous broadleaf species, other than *L. styraciflua*, were assumed to follow transpiration per unit leaf area of *L. styraciflua*. Based on previous sap flux studies, *L. styraciflua* has a reference stomatal conductance ($63\text{--}98 \text{ mmol m}^{-2} \text{ s}^{-1}$ at a reference $D = 1 \text{ kPa}$) similar to both *A. rubrum* and *L. tulipifera* (88 and $97 \text{ mmol m}^{-2} \text{ s}^{-1}$), other common hardwoods at this site (Oren

et al., 1999). Using the mean posterior transpiration time series from StaCC, pine and broadleaf transpiration was estimated at the plot level based on L of each.

For comparison to our estimate of scaled canopy transpiration, and to extend the transpiration time series, we used published values of leaf area and transpiration (T_P and T_B) for the years 1993–1996 (see Supplementary Material for approach) from data collected at this research site (Phillips & Oren, 2001). We did not conduct a full hydrologic balance calculation for these years, as the plot locations were not identical and the elevated CO_2 treatment from 1994 to August 1996 was employed in only plot 7. In 1997, environmental and sap flux measurements differed significantly in their collection method and were not available for the entire period, so this year was also excluded from analyses.

2.4 | Hydrologic balance modeling

In closed systems, water input, output, and storage should balance. Assuming negligible lateral inflows to soils of this upland site, due to the very mild slope (<5%), we employed a simple one-dimensional water balance for Duke FACE, with all variables treated as depths of water (Paul et al., 2003):

$$P = E_C + E_S + T_P + T_B + F_O + F_D + \Delta W_S, \quad (1)$$

where P is precipitation, E_C is evaporation of water intercepted by the canopy, E_S is evaporation from the ground surface, T_P is pine transpiration, T_B is broadleaf transpiration, F_O is overland flow, F_D is drainage flow, and ΔW_S is change in soil moisture over all depths. The measurement of P and calculation of T_P and T_B are discussed in the preceding sections. For purposes of analyses and discussion, $E = E_C + E_S$, $T = T_P + T_B$, $ET = E + T$, and $WY = F_O + F_D$.

E_C and E_S were modeled using the Penman-Monteith equation (Monteith, 1965) to estimate potential evaporation rate (E_P):

$$\lambda E = \frac{s(R_{\text{net}} - G) + \rho_a c_p D / r_a}{s + \gamma(1 + r_c / r_a)}, \quad (2)$$

where λ is the latent heat of vaporization, R_{net} is net radiation, γ is the psychrometric constant, s is the rate of change in saturation specific humidity with air temperature, G is surface heat flux (assumed to be zero), c_p is the specific heat capacity of air, r_c is canopy resistance and r_a is aerodynamic resistance. For evaporating water intercepted by the canopy and forest floor, r_c was assumed to be zero while r_a was assumed to be 20 s/m (Paul et al., 2003). R_{net} was measured in a single plot (Plot 1), with the partitioning of absorbed radiation between the canopy and ground surface modeled as a function of sun angle, pine L (L_P), and broadleaf L (L_B) for each plot, using a radiative transfer model (see Supplementary Information). Actual canopy evaporation was modeled as:

$$E_C = E_{P(C)} * \frac{W_C}{S_C}, \quad (3)$$

where $E_{P(C)}$ is potential evaporation of the canopy calculated after Equation (2) using the fraction of R_{net} absorbed by the canopy. W_C

is the water content of the canopy and S_C is the water storage capacity of the canopy, estimated as 0.3 mm per unit L_P and 0.5 per unit L_B (Hingston, Galbraith, & Dimmock, 1998; Paul et al., 2003).

E_S was calculated in a parallel manner to E_C , using a storage capacity (S_S) of 0.3 mm per Mg ha⁻¹ of forest floor mass (Paul et al., 2003; Raison & Khanna, 1982). Forest floor mass was estimated from Lichter et al. (2008), by CO₂ treatment, assuming asymptotic litter masses from data through 2005 were maintained through 2010. Because slopes at the site were mild (<5%), water in excess of S_S was allowed to pond up to a depth of the height of litter, estimated from litter mass using a bulk density of 0.44 Mg ha⁻¹ mm⁻¹. This value was based on the mean bulk density of loblolly litter (0.2 Mg ha⁻¹ mm⁻¹) and duff (0.6 Mg ha⁻¹ mm⁻¹), assuming the forest floor mass was composed of 40% litter and 60% duff (Ottmar & Andreau, 2007). Water exceeding this depth contributed to F_O . Pondered water was allowed to infiltrate into the first soil layer at a rate of 5.3 mm/hr based on the mean value obtained for this site in a previous study (Thompson, Harman, Heine, & Katul, 2010).

Soil moisture dynamics to 1 m depth were modeled based on the Richard's equation approach previously applied to this site (Oren, Ewers, Todd, Phillips, & Katul, 1998), using soil properties given in Table 1. The saturated hydraulic conductivity (K_S) used in the calculations was obtained for three mineral soil layers (A-C) to a depth of 0.9 m, at each quarter plot based on a constant head permeameter (Amoozegar, 1989). The model was parameterized from a relationship between saturated soil water potential (Ψ) and volumetric water content (θ) by obtaining b and saturated soil water potential (Ψ_S) from the soil water characteristic curve ($\Psi = -\Psi_S(\theta/\theta_S)^{-b}$), where θ_S is the saturated volumetric soil water content, estimated as total porosity (Clapp & Hornberger, 1978). The hydraulic conductivity at a given θ (K_θ) is then estimated as $K_\theta = K_S(\theta/\theta_S)^{-2b+3}$. The site soil-water characteristic curve for soil layers in the top 0.4 m was determined using a pressure plate extractor (Soilmoisture Equipment Corp., Goleta, CA, USA) with samples from two locations in each plot. Saturated soil moisture (θ_S) and saturated soil water potential (Ψ_S) for soils below 0.4 m were taken from a previous study at this site (Oren et al., 1998).

Half-hourly water fluxes between soil layers of 0.01 m thickness were estimated by numerically integrating Richard's equation:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left[K_\theta \left(\frac{\partial \Psi}{\partial z} + 1 \right) \right], \quad (4)$$

using a fourth-order Runge-Kutta method at a 30 s integration time step. Extraction of transpired water ($T_P + T_B$) from each soil layer was taken to be proportional to the product of fine root area and the quantity $(1 - 1e^{\chi\Psi/\Psi_{WP}})$, where Ψ_{WP} is the wilting point water potential, conservatively taken to be 2 MPa (Brady & Weil, 2002). Relative root area distributions were based on minirhizotron data collected at this site from 1998 to 2004 (Pritchard et al., 2008), assuming no further change occurred in distribution after 2004. The lower boundary condition at 1-m depth permitted drainage (i.e., contribution to F_D in Equation (1) of water above field capacity of this soil layer, taken to be 0.4 m³ m⁻³. Initial conditions for all layers in

each plot-year were taken as the ratio of measured soil moisture in the top 30 cm to porosity.

2.5 | Statistics and software

The hydrologic balance model was computed using R (R Core Team, 2016), as were all analyses and figures. The model was run independently for each plot or, after fertilization in 2004, half-plot. Each plot or half-plot run in this manner was treated as a sample unit for analysis of annual model outputs, with random effects accounting for variability between paired plot blocks and, after split-plot fertilization, whole-plots. For analyses of these values, we treated the study as three experiments over different time periods: (a) a comparison of AU and EU treatments from 1998 to 2010; (b) a comparison of AU and EU treatments from 1998 to 2004; and (c) a comparison of all four treatments from 2005 to 2010. While the first of these approaches leverages the most data for evaluating the effects of ECO₂ on these processes, the second approach uses only data before split-plot fertilization avoiding the potential impact of changing sample unit size.

We fit a series of nested mixed models for annual E , T , ET , and WY for these periods, selecting the best model for each using Bayesian Information Criterion (BIC). Maximal models included fixed effects for P , ECO₂, and, for 2005–2010, fertilization, as well as all interactions. Random effects were included for paired-plot blocks and, after split-plot fertilization, whole plots in all nested models. The ECO₂ and fertilization treatments were then evaluated against this best model using likelihood ratio χ^2 tests. Mixed models and resulting analyses used the LME4 (Bates, Mächler, Bolker, & Walker, 2014) and LMERTEST (Kuznetsova, Brockhoff, & Christensen, 2017) packages. The parametric bootstraps in Figure 7 assumed a normal distribution of values across plots within each year, using the sample mean and standard deviation for each treatment-year to simulate ratios between treatment-year means 10⁴ times.

3 | RESULTS

The study period was marked by variable climatic conditions, most notably two extremely dry years in 2007 and 2010 (precipitation less than 70% of the long-term mean), with 2007 having the highest values of T_A and D during the study period as well (Figure 1). Two other markedly dry years (2001, 2005) and two markedly wet years (1999, 2003) occurred during the study period. Not readily apparent from the annual values, the drought beginning in late 2001 continued into the growing season of 2002, followed by an ice storm in December 2002. This ice storm caused extensive canopy damage, as can be seen in the decrease in pine leaf area index (L_P ; Figure 2a) from 2002 to 2003 and the increase in the leaf area index of broad-leaf species (L_B ; Figure 2c) from 2002 to 2006 in response to greater light availability below the pine canopy. After 2006, L_P recovered to its former maximum and L_B ceased to increase, showing some indication of a decline in the final years of the study. Sap flux scaled transpiration of pine (T_P ; Figure 2b) did not respond as strongly to

disturbance as did L_p , nor did the variation in L_B directly translate to the variation in estimates of broadleaf transpiration (T_B ; Figure 2d). While a lack of replication precluded statistical analysis of the ECO_2 treatment in the prototype plot before 1997, T_p was not decreased relative to the reference plot despite similar L_p for the period 1993–1996 (Figure 2a,b).

Evaporation (E) from the canopy and forest floor was stable from 1998 to 2004, ranging from 318 to 386 mm (Figure 3) across treatments. The lowest values of E were observed in 2007, ranging from 288 to 301 mm across treatments. Transpiration at the canopy scale (T) varied from 351 to 553 mm across treatments, with the lowest values occurring during 2007. Total ET ranged from 696 to 894 mm/year from 1998 to 2006, followed by a decrease during the extreme drought of 2007 and an increase from 2008 to 2010. The lowest estimate of ET was 651 mm in the EU treatment in 2007 and the highest estimate was 996 mm in the EF treatment in 2008. Water yield (WY) showed a general pattern of decline during the study period, partly due to high WY in the high precipitation years of 1999 and 2003 occurring early in the study. Annual changes in total water content of the top meter of soil (ΔW_S) ranged from -144 to 98 mm across treatments from 1998 to 2009. Steep declines in ΔW_S were observed in 2010, ranging from -326 to -221 mm across treatments.

Because the response of ΔW_S in 2010 was extreme compared to other years, we compared modeled values to soil moisture measurements from the 0–300 mm soil depth at the daily and annual time

scales (Figure 4). The daily values show a very similar seasonal pattern and there are no significant differences between annual ΔW_S for this depth range in any treatment (t tests, $p > 0.24$ for all treatments). Note that deeper measurements of soil moisture were not made, but model outputs suggest that the greatest differences in soil moisture occurred below this depth (Supporting Information Figure S1). This prediction was corroborated by ocular observations of dry soil overlaying hardened clay at one-meter depth in two locations in each half-plot ($n = 32$) during root excavations for whole tree harvests in early 2011.

We fit a series of nested mixed models for annual E , T , ET , and WY for three periods (Table 2), selecting the best model for each by BIC. The ECO_2 and fertilization treatments were then evaluated against this best model (Table 3). For the entire 1998–2010 study period, we did not find a significant effect for ECO_2 on any of the annual outputs, while E , ET , and WY all increased with P . However, the effect of P was rather weak for E and ET , as can be seen by the low parameter values marginal pseudo- R^2 (R^2_M). On the other hand, P strongly effected WY , with a predicted change of 366 mm over the range of P values observed in the study period, which is 109% of the predicted WY at the long-term mean P . Most of the variance in WY was explained by P , as seen in the high R^2_M . If we evaluated ECO_2 effects for only the period preceding split-plot fertilization (1998–2004), we find a significant, but weak impact of ECO_2 on E , reducing it by 5.6 mm or 1.6% of the mean predicted value. As indicated by Figure 3, E , T , and ET did not show a strong response to P over this period, but WY did, showing a predicted change of 384 mm over the range of P observed during this period. After split-plot fertilization (2005–2010), we observed a response to P in all outputs, as well as a response to fertilization for T , ET , and WY . Fertilization impacts reduced T and ET , while increasing WY . However, the impacts were modest, ranging from -28.8 to 17.9 mm in magnitude, $<3\%$ of mean annual P . During this time period, the impact of P on WY was much weaker, likely because of very different responses in the two drought years of 2007 and 2010 (Figure 3), where 2007 exhibited greatly reduced WY while 2010 did not, exhibiting instead a large change in ΔW_S .

We also assessed the balance between ecosystem hydrological inputs and outputs for each period by fitting models for $ET + WY$ against P (Tables 2 and 3). There were no significant effects of ECO_2 or fertilization on this sum of outputs. The proportion of each output from the hydrological model (E , T , and WY), as it varied over the range of observed precipitation, is presented for 1998–2010 in the AU and EU treatments (Figure 5) and for 2005–2010 in all treatments (Figure 6). For 1998–2010 period, the contribution of ET to this sum decreased with increasing P , ranging from 91% at the lowest observed P to 62% at the highest P . The partitioning of ET into its components did not respond as strongly to P , with E accounting for $\sim 45\%$ of ET across the observed range of P . For the 2005–2010 period, the proportion of total outputs attributed to ET varied less, accounting for 75%–82% across fertilization treatments and across the range of P . During this period, E accounted for 45%–50% of ET across fertilization treatments and across the range of P .

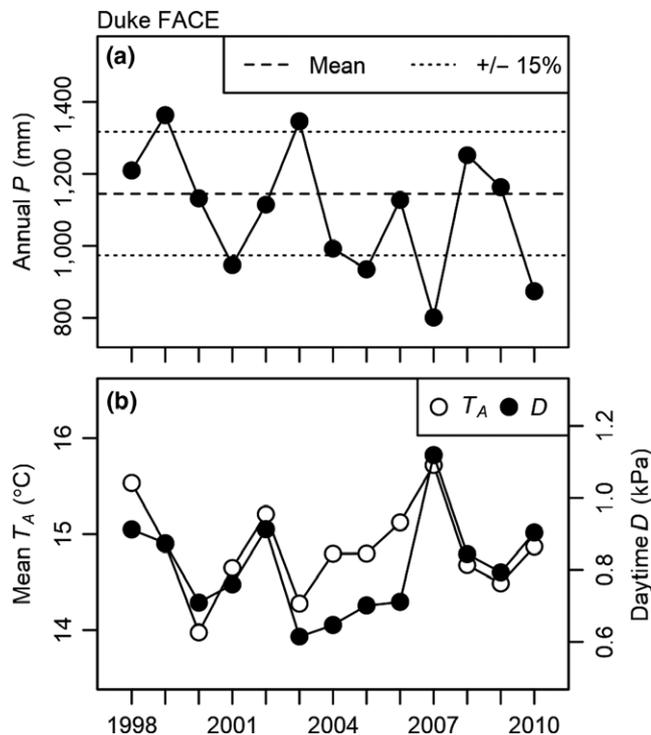


FIGURE 1 Measured site-level hydrological model inputs by year: (a) total annual precipitation (P) with lines indicating 111-year mean $\pm 15\%$, (b) mean annual air temperature (T_A), and mean daytime vapor pressure deficit (D)

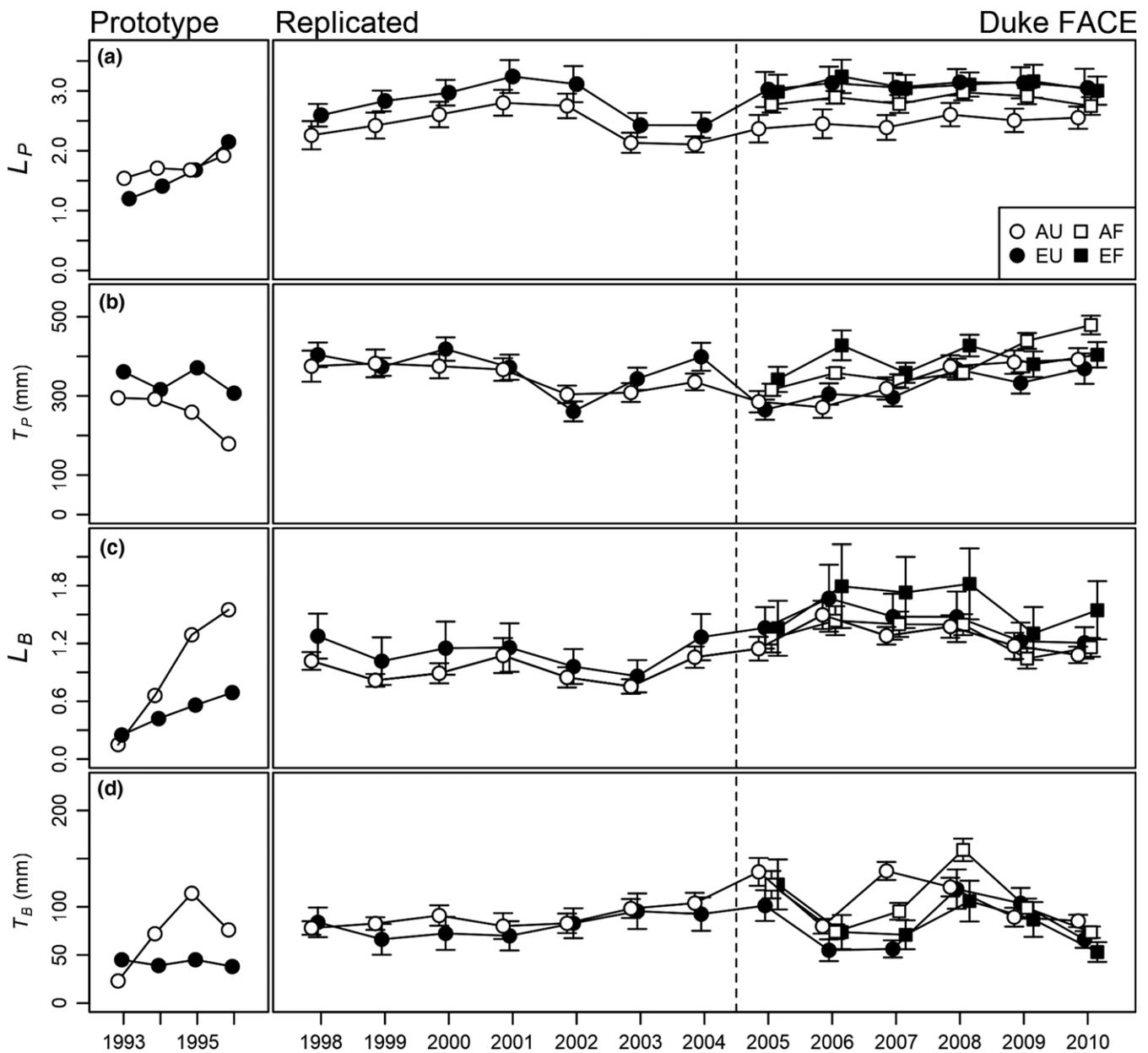


FIGURE 2 Measured plot-level hydrological model inputs by year and treatment: projected leaf area index (L) and transpiration (T) for pines and broadleaf species (P and B subscripts, respectively). Left-hand panels represent prototype measurement period with unreplicated measurements, while right-hand panels represent experimental period with replicated measurements. Bars represent standard error across plots ($n = 4$). Abbreviations for treatments: AU—ambient $[\text{CO}_2]$ unfertilized, EU—elevated $[\text{CO}_2]$ unfertilized, AF—ambient $[\text{CO}_2]$ fertilized, EF—elevated $[\text{CO}_2]$ fertilized. Dotted vertical line indicates the establishment of fertilization treatment in January, 2005. Treatment symbols are slightly staggered to increase clarity

Positive intercepts and slopes less than one for the uppermost line ($ET + WY$) in Figures 5 and 6 indicate that the model tends to predict net soil water deficits (negative ΔW_S) in years with low P and net storage increases (positive ΔW_S) in years with high P . The value of P where this line intersects the 1:1 line is where no net change in soil water storage is predicted to occur ($\Delta W_S = 0$). This occurs at 1,177 mm for 1998–2010 in the AU and EU treatments and 1,095 mm for 2005–2010 in all treatments, both within 50 mm of the long-term average P for this site of 1,145 mm. The slope is not significantly different from one (Wald χ^2 test, $p = 0.109$) nor is

the intercept is significantly different from zero (Wald χ^2 test, $p = 0.10$) for the 1998–2010 period when only the AU and EU treatments are considered (Figure 5). However, both parameters differ from these values significantly in the 2005–2010 period when considering all treatments (Figure 6; Wald χ^2 tests, $p < 0.001$).

Annual treatment level means and their standard deviations (Supporting Information Tables S1 and S2) were used in a parametric bootstrap of the flux response ratios—water balance components (E , T , ET , and WY) of each treatment normalized by that of the AU plots—for each year, as well as across years (Figure 7). The ratios varied

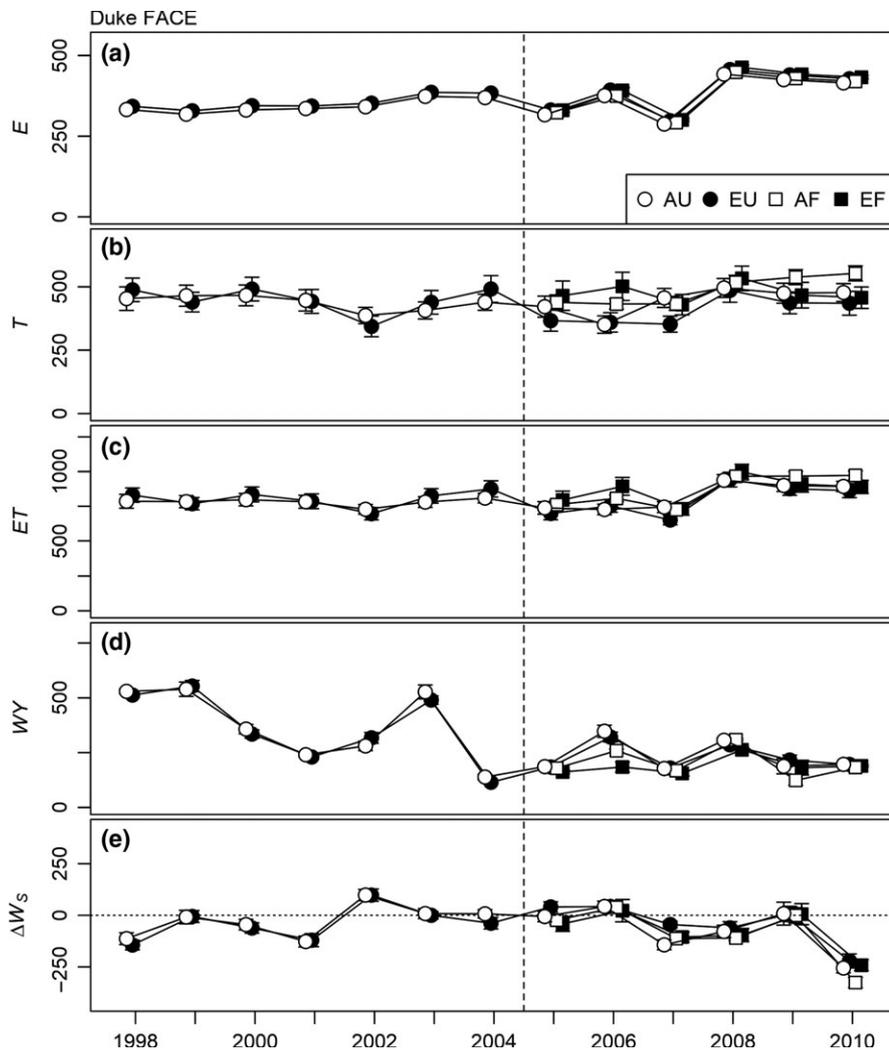


FIGURE 3 Partitioning of annual precipitation (mm) in each treatment into: transpiration (T), evaporation (E) from canopy and forest floor, evapotranspiration (ET , sum of E and T), water yield (WY , the sum of overland flow and drainage), and changes in total water content of the top meter of soil (ΔW_s). Abbreviations for treatments: AU—ambient $[CO_2]$ unfertilized, EU—elevated $[CO_2]$ unfertilized, AF—ambient $[CO_2]$ fertilized, EF—elevated $[CO_2]$ fertilized. Dotted vertical line indicates the establishment of fertilization treatment. Treatment symbols are slightly staggered to increase clarity

over time and some ratios did not have 95% confidence intervals that overlapped unity in certain years. The tendency for slightly higher E in ECO_2 plots (Table 2) can be seen in this plot, but the magnitude of this effect is small ($\sim 5\%$). The uncertainty of WY was very high in low P years, as WY in the AU treatment (the flux ratio denominator) approached zero. No other consistent pattern between such ratio and annual precipitation or the other meteorological drivers found in Figure 1 emerged. Across years, however, these flux response ratios all included unity within their 95% confidence intervals.

4 | DISCUSSION

We did not find that elevated atmospheric CO_2 concentration (ECO_2) created large or consistent differences in stand evapotranspiration (ET) or water yield (WY) under native or enhanced soil fertility (Figure 7). While both ET and WY were found to decrease and increase, respectively, with fertilization (Tables 2 and 3), this effect was small ($<3\%$ of mean annual precipitation). Furthermore, the long-term averages suggest a ratio very close to unity for the main partitioning of water into ET or WY for all treatments relative to the

control (Figure 7). While evaporation (E) was decreased by ECO_2 in the first 7 years of the study (Table 2), this effect was negligible ($<1\%$ of mean annual precipitation). Due to large interannual variation resulting from structural changes in the canopy and small sample sizes ($n = 4$), long-term (1998–2010) averages may lack the resolution to resolve these sorts of small differences. However, it is clear that ECO_2 did not create notable differences in stand ET or WY under either native or enhanced soil fertility, despite a 20% and 13% increase in leaf area index, respectively. Data from the prototype period preceding the replicated experiment (Figure 2) and short-term manipulations of $[CO_2]$ after the experiment (Torngern et al., 2015) are also consistent with an “indirect” effect on stomatal conductance that maintained a similar stand-level ET , despite large structural changes under the ECO_2 and fertilization treatments.

The often stated prediction that transpiration will decrease under ECO_2 is grounded in commonly observed reductions in stomatal conductance per unit leaf area (Ainsworth & Rogers, 2007; Medlyn et al., 2001), predicted to result in a greater savings of water in ecosystems with well-coupled canopies (Woodward, 1990). However, this reduction in stomatal conductance is weaker or less often observed in forests than in grasslands and crops, in conifer forests

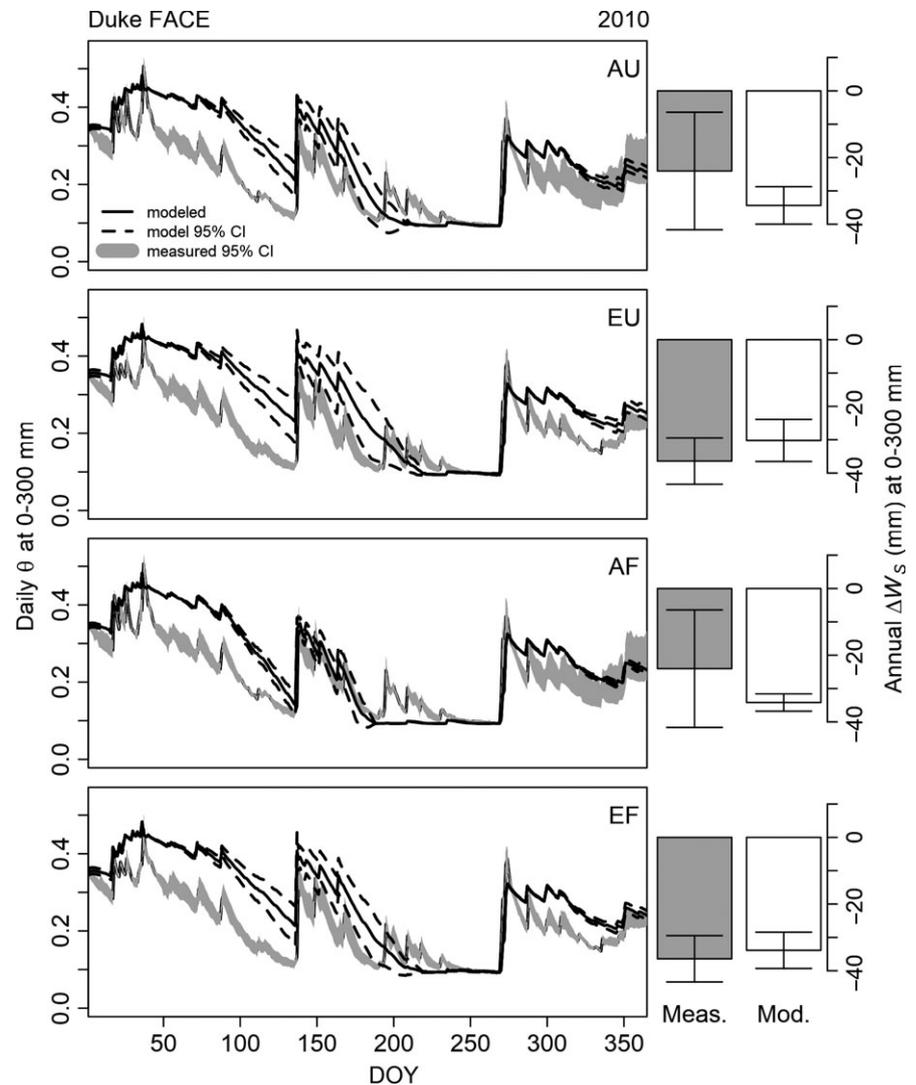


FIGURE 4 Measured and modeled mean volumetric water content (θ) for 0–300 mm depths by day of year (DOY) for 2010. The dashed lines for the modeled values and the width of gray lines for the measured values indicate 95% confidence interval ($n = 4$ plots). The bar plot in right panel shows the change in total soil water content (S) from the first to last measurement of the year, with bars representing 95% confidence intervals ($n = 4$)

than in deciduous ones, and in mature stands than in young, aggrading stands (Medlyn et al., 2001; Pataki et al., 1998; Saxe, Ellsworth, & Heath, 1998; Wullschleger, Tschaplinski, & Norby, 2002).

In an elevated CO_2 experiment conducted on a broadleaf species (*Liquidambar styraciflua*) at the Oak Ridge FACE, persistent stomatal closure was observed (Warren, Norby, & Wullschleger, 2011), resulting in reduced transpiration and model projections of increased WY (Warren, Pötzelsberger, et al., 2011). However, in stands with different mixtures of *Populus* and *Betula* species at the Aspen FACE, observations of stomatal closure in the initial years of study (Noormets et al., 2001) were not found to persist after canopy closure (Uddling, Teclaw, Pregitzer, & Ellsworth, 2009) and transpiration increased under ECO_2 as a result of increases in leaf area (L). Indeed, a synthesis of FACE studies suggests that ECO_2 increases L in sites with low L under ambient $[\text{CO}_2]$ (ACO_2), such as Aspen FACE, but not those with high L under ACO_2 , such as Oak Ridge FACE, with Duke Forest FACE being an intermediate case (Norby & Zak, 2011). Our results demonstrate that ECO_2 and fertilization-induced increases in L (McCarthy et al., 2007), when not nullified by drought or storms, had nearly as large a contribution as any reduction in

stomatal conductance on the ET response at Duke FACE. It must be noted that early results from a FACE experiment in a *Eucalyptus* forest in Australia show no increase in L with ECO_2 despite rather low L under ambient conditions (Duursma et al., 2016). However, the subtropical climate of this site and its limited water supply may set greater limits on the potential L that can be sustained than the temperate sites mentioned above.

The lack of response of water partitioning between ET and WY to ECO_2 may be a surprising result, given the many documented changes in this ecosystem over the course of the experiment. However, the directionality of many changes observed under ECO_2 is consistent with structural and physiological adjustments that conserve the magnitude of ET despite notable changes in stand structure. Our results are consistent with findings from this site that decreases in stomatal conductance under ECO_2 and fertilization were roughly proportional to increases in L (Ward et al., 2013). The “indirect” nature of reduction in stomatal conductance under ECO_2 , as opposed to stomatal closure induced directly by increases in atmospheric CO_2 , is consistent with the reduced hydraulic supply of water to leaves based on allometry (Ward et al., 2013), as well as

TABLE 2 Statistical models for evaporation (E , mm), transpiration (T , mm), evapotranspiration (ET , mm), and water yield (WY , mm) observations at the Duke FACE site for the entire study period (1998–2010) and the period with (2005–2010) split-plot fertilization treatments. Models were selected by Bayesian Information Criterion (BIC) from a set of nested models with fixed effects for precipitation (P , mm), elevated $[CO_2]$ (C), and, for 2005–2010, fertilization (F). Random effects were included for block and, for 2005–2010, whole plots. The standard errors for block and whole plots are σ_B and σ_P , respectively, while σ_R is residual standard error. The variance described by fixed effects is indicated by the marginal pseudo- R^2 (R^2_M), while the variance described by fixed and random effects is indicated by the conditional pseudo- R^2 (R^2_C)

Years	Equation	Parameter	Estimate (SE)	σ_B	σ_P	σ_R	R^2_M	R^2_C	
1998–2010	$E = \beta_2 P + \beta_1$	β_1	293.5 (29)	<0.01		45.2	0.06	0.06	
		β_2	0.065 (0.026)						
	$T = \beta_1$	β_1	435.0 (19.0)	36.7		52.2		0.33	
	$ET = \beta_2 P + \beta_1$	β_1	670.4 (52.7)	38.0		76.6	0.05	0.24	
		β_2	0.118 (0.044)						
	$WY = \beta_2 P + \beta_1$	β_1	−408.6 (54.4)	19.2		83.5	0.63	0.65	
		β_2	0.651 (0.048)						
	$ET + WY = \beta_2 P + \beta_1$	β_1	126.5 (77.7)	<0.01		74.0	0.77	0.77	
		β_2	0.893 (0.067)						
	1998–2004	$E = \beta_2 C + \beta_1$	β_1	348.8 (2.8)	<0.01		21.0	0.07	0.07
β_2			−5.7 (2.8)						
$T = \beta_1$		β_1	442.7 (18.7)	35.2		46.4		0.36	
$ET = \beta_1$		β_1	791.5 (19.9)	37.3		50.9		0.35	
$WY = \beta_2 P + \beta_1$		β_1	−697.4 (70.9)	17.3		60.3	0.80	0.81	
		β_2	0.921 (0.060)						
$ET + WY = \beta_2 P + \beta_1$		β_1	261.8 (50.9)	3.9		79.2	0.73	0.73	
		β_2	0.770 (0.046)						
2005–2010		$E = \beta_2 P + \beta_1$	β_1	122.2 (26.5)	<0.01	<0.01	41.2	0.52	0.52
			β_2	0.256 (0.026)					
	$T = \beta_3 P + \beta_2 F + \beta_1$	β_1	338.0 (35.8)	23.0	20.9	51.4	0.23	0.44	
		β_2	−27.2 (5.2)						
		β_3	0.112 (0.032)						
	$ET = \beta_3 P + \beta_2 F + \beta_1$	β_1	460.2 (54.9)	25.4	<0.01	83.0	0.38	0.43	
		β_2	−28.8 (8.5)						
		β_3	0.369 (0.051)						
	$WY = \beta_3 P + \beta_2 F + \beta_1$	β_1	−9.8 (32.8)	15.4	<0.01	49.5	0.38	0.43	
		β_2	17.9 (5.0)						
		β_3	0.218 (0.031)						
	$ET + WY = \beta_2 P + \beta_1$	β_1	450.4 (52.4)	<0.01	<0.01	81.3	0.59	0.59	
		β_2	0.587 (0.050)						

reductions in light within the canopy (Kim, Palmroth, Therezien, Stenberg, & Oren, 2011) and reduced hydraulic conductivity in the needles of *P. taeda* (Domec et al., 2009; Domec, Palmroth, et al., 2016). An experiment conducted at Duke Forest FACE confirmed the lack of T response to short-term fluctuations in atmospheric CO_2 (up to 1.8 of ambient), which is consistent with these indirect mechanisms, but not with stomatal closure induced directly by ECO_2 in either of the main species at the site (Tor-ngern et al., 2015). We also see no indication of reduced transpiration for pine in unrepliated prototype experiment (Figure 2b 1993–1996), suggesting that stomatal conductance was not reduced prior to changes in L . While the main hardwood species in the stand (*L. styraciflua*) was shown to

reduce stomatal conductance at the leaf level in response to ECO_2 when comparing leaves with similar light exposure (Herrick et al., 2004), changes in structure may lead to different effects at the canopy scale. In particular, the damage and recovery of the pine-dominated overstory from drought and ice storm disturbance may have led to greater spatial and interannual variability in the later years of study (Figure 3).

The lack of a large ET response observed with the three main droughts in this study during 2001–2002, 2007, and 2010 (Figures 1 and 3) belies the observation of strong declines in stomatal conductance and leaf conductivity in the 2007 drought (Domec et al., 2009). Although decreased precipitation in a drought reduces the

TABLE 3 Results of likelihood ratio χ^2 tests for elevated CO₂ (C) and fertilization (F) treatment effects, relative to selected statistical models from Table 2 for each model output: evaporation (E), transpiration (T), evapotranspiration (ET), water yield (WY), and total ecosystem hydrological output (ET + WY). Bold values indicate variables included in models in Table 2

Years	Variable	Treatment	<i>p</i>
1998–2010	E	C	0.152
	T	C	0.203
	ET	C	0.976
	WY	C	0.710
	ET + WY	C	0.505
1998–2004	E	C	0.043
	T	C	0.412
	ET	C	0.110
	WY	C	0.629
	ET + WY	C	0.672
2005–2010	E	C	0.114
		F	0.698
	T	C	0.110
		F	<0.001
	ET	C	0.481
		F	<0.001
	WY	C	0.380
		F	<0.001
	ET + WY	C	0.213
		F	0.186

plant available soil moisture, the concomitant increase in atmospheric vapor pressure deficit (*D*, Figure 1) driving transpiration may have attenuated interannual variation in *ET* in our study, as was found in a nearby unmanaged broadleaf forest (Oishi et al., 2010). This is consistent with the modest *ET* responses found for this broadleaf stand (3%–12%) and the larger pine forest in which Duke

Forest FACE site was located (8%–13%) to the 2001–2002 and 2007 droughts (Novick et al., 2015). However, concurrent CO₂ flux estimates by Novick et al. (2015) suggest that carbon assimilation of these forests was much more sensitive to drought than was *ET*, especially the pine forest, highlighting the role of stomatal closure in this process (Oren et al., 1998; Tor-ngern et al., 2015). Thus, observations of conserved *ET* are not evidence for a lack of differing water stress under different treatments or under varying environmental conditions.

Water use efficiency (*WUE*), as a ratio of gross primary productivity (*GPP*) to *ET*, is generally expected to increase as atmospheric concentrations of CO₂ rise, due to both increases in *GPP* and possible decreases in *ET* (Keenan et al., 2013). A study that applied 11 state-of-the-art ecosystem models to data from Duke Forest FACE concluded that the models generally captured the increase in *WUE* with ECO₂ well, but underpredicted both *GPP* and *ET* ratios between ECO₂ and ACO₂ (De Kauwe et al., 2013). Thus, many commonly used ecosystem models may be capturing the *WUE* effect of CO₂ for the wrong reasons, predicting changes in both components where *GPP* is indeed increasing but *ET* is actually remaining the same. It should be mentioned that the same study found that the *WUE* increase with ECO₂ at Oak Ridge FACE was underpredicted by the same set of models, although the *GPP* responses were generally accurate, indicating that the magnitude of decrease in *ET* with ECO₂ was underpredicted. What is clear from the results of FACE studies is that the responses of forests to ECO₂ are not the same across forest types, but changes in *L* may be an important factor to consider in understanding the variation in responses (McCarthy, Oren, Finzi, et al., 2006; Norby & Zak, 2011; Norby et al., 2005).

The FACE technology employed in this study alters the atmospheric concentration of CO₂, but not the environmental drivers of the hydrologic cycle expected to change concomitantly with CO₂ levels. While we did observe a range of environmental conditions during this study (Figure 1), we do not see the effects of consistent

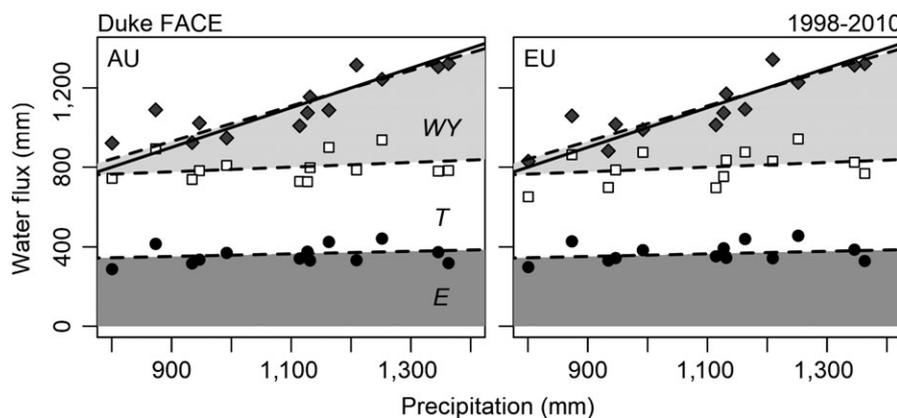


FIGURE 5 Partitioning of ecosystem outputs versus annual precipitation, including evaporation from canopy and forest floor (*E*), transpiration (*T*), and water yield (*WY*) for the years 1998–2010. The solid line represents a 1:1 relationship between ecosystem inputs and outputs, the imbalance of which represents changes in total soil column water content calculated by the hydrological model. Dashed lines represent the mixed models for *E*, total evapotranspiration (*ET*), and total hydrological outputs (*ET* + *WY*) from Table 2. Abbreviations for treatments: AU—ambient [CO₂] unfertilized, EU—elevated [CO₂] unfertilized.

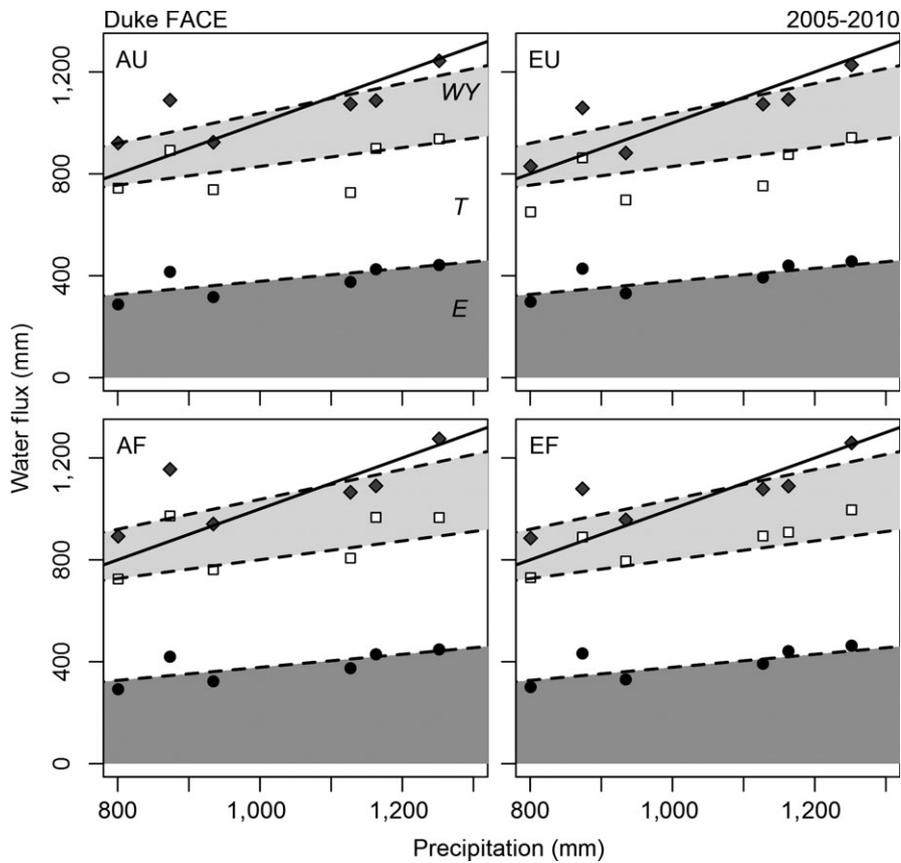


FIGURE 6 Partitioning of ecosystem outputs versus annual precipitation, including evaporation from canopy and forest floor (E), transpiration (T), and water yield (WY) for the years 2005–2010. The solid line represents a 1:1 relationship between ecosystem inputs and outputs, the imbalance of which represents changes in total soil column water content calculated by the hydrological model. Dashed lines represent the mixed models for E, total evapotranspiration (ET), and total hydrological outputs (ET + WY) from Table 2. Abbreviations for treatments: AU—ambient [CO₂] unfertilized, EU—elevated [CO₂] unfertilized, AF—ambient [CO₂] fertilized, EF—elevated [CO₂] fertilized.

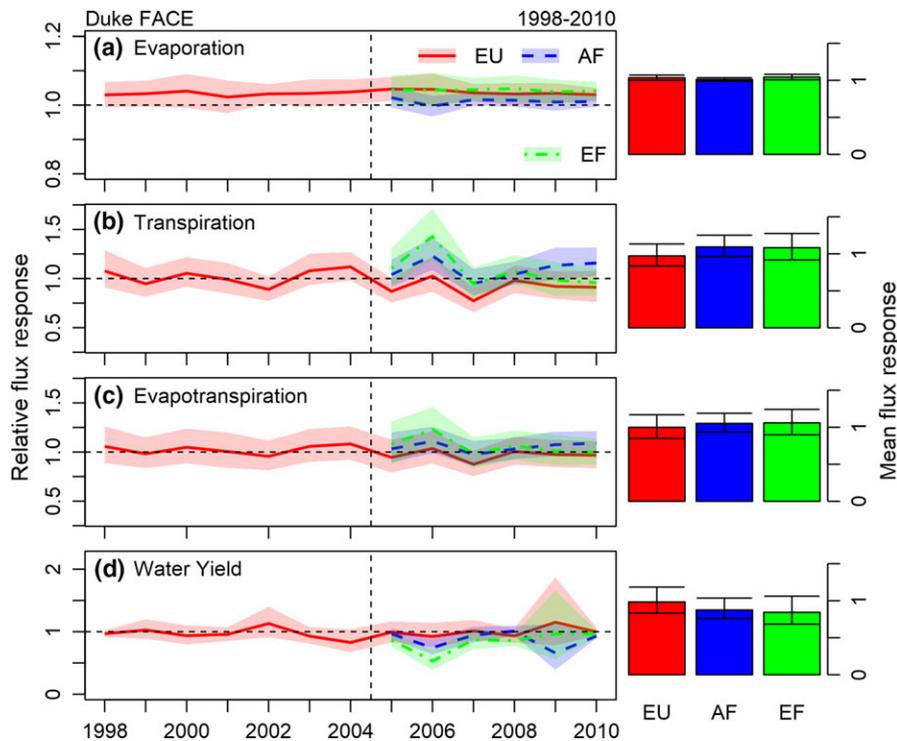


FIGURE 7 Flux response ratios for each treatment, relative to the ambient [CO₂] unfertilized control plots, for the years 1998–2010 (left column) and the mean ratio across year (right column). Abbreviations for treatments: AU—ambient [CO₂] unfertilized, EU—elevated [CO₂] unfertilized, AF—ambient [CO₂] fertilized, EF—elevated [CO₂] fertilized. Dotted vertical line indicates the establishment of fertilization treatment. Shaded polygons are 95% confidence intervals for each treatment year of the ratio EU/AU from a parametric bootstrap assuming normally distributed plot-level values ($n = 4$) for each year, bars in the right column represent means of these confidence intervals across years

directional changes that may impact forest hydrological cycling, such as an increase in the atmospheric demand for water (Novick et al., 2016). The response of such forests to drought conditions, which

both decrease the supply of water and increase the atmospheric demand for it, is a crucial area of study in the context of predictions of widespread drought-induced mortality in many of the world's

forested areas (Allen et al., 2010; McDowell et al., 2015, 2016). Even at Oak Ridge FACE, where ECO_2 was observed to reduce transpiration in most years, earlier leaf senescence was observed under ECO_2 than ACO_2 during severe drought (Warren, Norby, et al., 2011). Drought vulnerability in *P. taeda* stands has been suggested to be higher under ECO_2 (Domec, Smith, & McCulloh, 2017) and when grown with fertilization (Ewers et al., 2000; Ward et al., 2015), which is rapidly becoming a standard forestry practice in this region (Albaugh, Allen, & Fox, 2007). Pine forests have also been found to be more vulnerable to drought than unmanaged broadleaf stands in this region (Domec et al., 2015; Stoy et al., 2006).

At the stand scale over the 13 years, we found that the major response to variation in annual precipitation was in WY (Figure 5) and not ET or its component fluxes. Indeed, water yield was minimal in the years with the lowest precipitation, consistent with observations from a nearby broadleaved deciduous forest and water flows downstream (Oishi et al., 2010). Thus, we would expect that ECO_2 would have minimal impacts on downstream ecosystems, such as wetlands and streams, when compared to other environmental drivers, at least within the observed range of variation (Figure 1). More frequent or extended droughts of the magnitude observed in this study (e.g., 2007 or 2010) may have large impacts on downstream ecosystems, which we would not predict to be ameliorated by a rise in CO_2 in *P. taeda*-dominated watersheds. Projections of future climate in the southeastern United States suggest that atmospheric demand for water may rise faster than the supply of precipitation, but a large degree of uncertainty remains in such predictions (Seager, Tzanova, & Nakamura, 2009).

Across the globe, however, droughts in forest ecosystems are intensifying (Allen, Breshears, & McDowell, 2015) and widespread tree mortality is already being observed as a result (Allen et al., 2010; McDowell et al., 2015, 2016). Our results support the generality that, regardless of the rate of stand development or the influence of available resources on that rate, once canopies achieve high L, transpiration becomes a fairly conservative quantity (Ohta et al., 2008; Oishi et al., 2010; Roberts, 1983; Wilson & Baldocchi, 2000). If evaporative demand (e.g., D) rises with $[\text{CO}_2]$ and temperature of the atmosphere, the reduced stomatal conductance implied by this relatively invariant transpiration may counteract the positive effect of rising $[\text{CO}_2]$ on tree growth and survival (Novick et al., 2016). Given the global range of conifers similar to *P. taeda* (Tor-ngern et al., 2017), our results also indicate that recent observations of increased global streamflow cannot be attributed to decreases in ET across all ecosystems (Betts et al., 2007; Gedney et al., 2006). Our results, taken in context of other forest FACE studies (Duursma et al., 2016; Uddling et al., 2009; Warren, Pötzelberger, et al., 2011), exhibit that forest L, ET, and WUE responses to ECO_2 vary by dominant species, site quality, and climatic regime. Given the mixed performance of existing models to represent this diversity of responses (De Kauwe et al., 2013) and the large volumes of data collected by such long-term experiments, there is a great need for model–data synthesis activities (Norby et al., 2016; Thomas et al.,

2017) to improve our understanding of terrestrial vegetation feedbacks to the global carbon and water cycles.

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