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Key Points:

- Suppressed heterotrophic respiration by drought and fertilization amplified carbon sequestration responses compared to those in productivity
- Carbon sequestration efficiency increased up to threefold under both drought and fertilization
- Trade-off between biomass production and carbon sequestration has implications for forest management for climate mitigation purposes

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Heterotrophic Respiration and the Divergence of Productivity and Carbon Sequestration

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Abstract Net primary productivity (NPP) and net ecosystem production (NEP) are often used interchangeably, as their difference, heterotrophic respiration (soil heterotrophic CO_2 efflux, R_{SH} = NPP−NEP), is assumed a near-fixed fraction of NPP. Here, we show, using a range-wide replicated experimental study in loblolly pine (*Pinus taeda*) plantations that R_{SH} responds differently than NPP to fertilization and drought treatments, leading to the divergent responses of NPP and NEP. Across the natural range of the species, the moderate responses of NPP (+11%) and R_{SH} (−7%) to fertilization combined such that NEP increased nearly threefold in ambient control and 43% under drought treatment. A 13% decline in R_{SH} under drought led to a 26% increase in NEP while NPP was unaltered. Such drought benefit for carbon sequestration was nearly twofold in control, but disappeared under fertilization. Carbon sequestration efficiency, NEP:NPP, varied twofold among sites, and increased up to threefold under both drought and fertilization.

Plain Language Summary Two metrics of ecosystem productivity—vegetation biomass accumulation (net primary production, NPP) and net ecosystem carbon gain (NEP)—are often used interchangeably, as their difference, heterotrophic respiration, is assumed a relatively constant fraction of the former. Here, we show that soil heterotrophic respiration responds to water availability (a major climate change variable) and nutrient availability (a major management factor) differently than does NPP, leading to the divergence of NPP and NEP responses to water and nutrient availability.

1. Introduction

The terrestrial biosphere cycles about 15.7% of atmospheric carbon each year, with roughly equal amounts being assimilated through photosynthesis and released through respiration (Baldocchi & Penuelas, 2019). The climate mitigation benefit of biological carbon sequestration can arise if more of the assimilated carbon enters long-turnover pools in vegetation and soil than is released from them. However, the expansion of human land use continues to erode the area of carbon-rich old-growth forests (FAO, 2012) and a growing fraction (about 7%) are managed (Hansen et al., 2013) at increasing intensity (Fox et al., 2007). The intensifying use of the Earth's ecosystems has negative implications for biological carbon sequestration for two reasons. First, ecosystem management typically involves the replacement of ecosystems with high standing biomass and moderate productivity with those with low standing biomass and high productivity (Erb et al., 2016). As a result, human land use has doubled the carbon turnover rate compared to undisturbed

natural systems (Erb et al., 2016). Second, the increasing disturbance frequency that accompanies intensive land management stimulates heterotrophic activity and the mineralization rate of existing soil C pools (Lewis & Wheeler, 2019; Noormets et al., 2015). Thus, land-use intensification tends to increase both net primary productivity (NPP) and R_{SH}, with unclear consequences for net ecosystem production (NEP).

The primary management practice in cultivated lands, including forests, is fertilization (Galloway et al., 2008; Magnani et al., 2007; Noormets et al., 2015), that increases productivity and shifts biomass allocation toward aboveground tissues (Chen et al., 2013). In addition, even non-fertilized ecosystems have experienced increased nutrient availability due to the global reach of atmospheric deposition of industrial pollution (Galloway et al., 2008). The lower carbon cost of belowground resource acquisition under fertilization allows for increased aboveground growth and productivity. The extent to which this increased observable productivity (Campbell et al., 2017) translates to a greater land carbon sink remains a topic of investigation (Xia et al., 2017), and the multitude of processes involved suggest a possible divergence between NPP and NEP. First, the increased aboveground and decreased belowground detritus production are unlikely to simply offset one another in terms of soil C inputs, as the differences in chemical composition and physical protection from decomposer and invertebrate communities allow belowground detritus to persist longer in the soil than aboveground detritus (Adamczyk et al., 2019; Clemmensen et al., 2013; Godbold et al., 2006). Second, increased nutrient availability in the soil tends to suppress microbial activity through stoichiometric and substrate availability effects (Averill & Waring, 2018) and symbiotic interactions (Kuzyakov & Gavrichkova, 2010). Recent analyses have also demonstrated tight coupling between allocation and carbon use efficiency (the ratio of NEP to gross primary production or gross photosynthesis) (Campioli et al., 2015; Fernandez-Martinez et al., 2014; Vicca et al., 2012) at high nutrient availability, reflective of the reduced respiratory and allocation costs associated with both root and rhizosymbiont support (Treseder, 2004; Treseder et al., 2007).

Alongside increasing anthropogenic management pressures on the biosphere (Erb et al., 2016; Krausmann et al., 2013), the intensifying hydrological cycle is also leading to more frequent and more intensive drought events (Huntington, 2006). The universally negative effect of drought on plant productivity is assumed to translate to a lower land carbon sink (Kolus et al., 2019), even though its interactions with changing nutrient availability and other global change factors (including drought, but also elevated CO_2 and temperature) are only beginning to be explored (Nogueira et al., 2018; Samuelson et al., 2018; Siebert et al., 2019; Ward et al., 2015). We have shown earlier that the fertilization-induced decrease in the drought sensitivity threshold at the VA study site of this replicated experiment was detectable in the sensitivity of canopy conductance to water availability and evaporative demand (Ward et al., 2015). This change in conductance was attributed to a lower ratio of root area to leaf area, which is also expected to lead to lower soil autotrophic and heterotrophic respiration, and modulates the response of NEP to drought. Using a range-wide replicated experiment of water and nutrient availability in loblolly pine (*Pinus taeda*) plantations (Will et al., 2015), the current study set out to quantify the drought sensitivity of NPP, $R_{SH,}$ and NEP at different nutrient availabilities. We show consistent divergence of NPP and NEP responses to drought, and the amplified response to fertilization as a result of modest and predictable responses of R_{SH}.

2. Materials and Methods

2.1. Study Domain and Sites

The study was carried out in three replicated full factorial experiments of nutrient and water availability, with two levels of each, established as a part of the PINEMAP study (Pine Integrated Network: Education, Mitigation, and Adaptation Project, www.pinemap.org). The study sites were located in the climatic extremes of the natural range of loblolly pine (Figure 1a)—Taylor County, Florida (30°12′22″N, 83°52′12″W), McCurtain County, Oklahoma (34°01′47″N, 94°49′23″W), and Buckingham County, Virginia (37°27′37″N, 78°39′50″W). Each experiment consisted of four replicate plots (800 m^2 treatment area, with measurements constrained to the central 300 m^2) of ambient control (C), fertilization (F), throughfall reduction or drought (D), and combination (FD) treatment. The throughfall reduction was achieved with troughs covering 30% of the plot area (Figure 1b), and removing 30% of the throughfall (Bracho et al., 2018; Will et al., 2015). The main site climate, soil, and vegetation characteristics are shown in Table 1. The fertilization treatment targeted optimal mineral nutrient availability for growth (Fox et al., 2007), and included nitrogen (urea

Figure 1. The native range of loblolly pine (shaded area) in the Southeast United States and the locations of the through-fall reduction and fertilization experiments (green, left). Throughfall reduction troughs (−30%) at the Virginia study site (right). Photo: A. Laviner.

at 432 kg ha^{-1}), phosphorus (diammonium phosphate at 140 kg ha^{-1}), potassium (potash at 112 kg ha^{-1}). Micronutrients were supplied as granular oxysulfate micronutrient mix (Southeast Mix, Cameron Chemicals, Inc., Virginia Beach, VA, USA) at a rate of 22.4 kg ha^{-1}, which contained 5% boron, 2% copper, 6% manganese, 6% sulfur, and 5% zinc. The fertilizers were broadcast applied by hand in March and April of 2012 (Will et al., 2015).

2.2. Measurements

Tree biomass, productivity, soil total, and heterotrophic respiration were measured as described in Bracho et al. (2018). Briefly, the diameter at breast height and height of all trees in the core area of the treatment plots were measured each winter, and the annual biomass increment was calculated using allometric

Table 1
Site Climate, Soil, and Vegetation Characteristics in 2011, Before the Start of the Throughfall Exclusion Treatments in the Summer of 2012. Foliar N was measured in the summer of 2012, following fertilizer application

	Florida	Oklahoma	Virginia
Climate and site characteristics			
MAT (°C)	19.4	16.6	13.6
MAP (mm)	1,450	1,300	1,120
Soil texture (0–30 cm)	Fine sand	Fine sandy loam	Silty clay loam
Soil [C] (mg g^{-1})	20.5	13.3	37.4
Soil [N] (mg g^{-1})	0.73	0.80	1.30
Vegetation characteristics			
Age (yr)	9	5	10
Tree density (stems ha^{-1})	1,720 ± 87	1,610 ± 102	789 ± 68
Basal area (m^2 ha^{-1})	22.4 ± 2.2	1.8 ± 0.3	13.2 ± 0.7
Height (m)	10.5 ± 0.5	2.9 ± 0.15	8.8 ± 0.2
Diameter (cm)	12.5 ± 0.7	3.6 ± 2.9	14.4 ± 0.5
Foliar [N] (%)[a]			
C and D	1.38 ± 0.05	1.29 ± 0.03	1.18 ± 0.01
F and FD	1.58 ± 0.02	1.47 ± 0.03	1.70 ± 0.06

Note. Vegetation characteristics are shown as the mean ± SD of four replicated plots of each of the four treatments.
[a]C, D, F, and FD refer to the control, drought, fertilization, and fertilization plus drought treatments.

relationships (Gonzalez-Benecke et al., 2014, 2016). Aboveground net primary production (ANPP) was calculated as the sum of woody biomass increment plus litterfall, belowground net primary production (BNPP) was calculated as the increment of coarse roots, and total net primary production (TNPP) was their sum. Soil CO_2 efflux was measured on three randomly located locations in each treatment plot, using LI-8100, LI-6400, or LI-6200 (Licor, Lincoln, NE, USA) infrared gas analyzers, and paired polyvinylchloride collars. For total soil CO_2 production, 10-cm collars were inserted 2–5 cm into the ground, and for root-excluded heterotrophic CO_2 production 32–35 cm collars were inserted 30–33 cm into the ground (Bracho et al., 2018). The similarity of soil CO_2 efflux between paired shallow and deep collar locations was verified before collar installation, and the heterotrophic fraction estimate was corrected for the initial difference. Heterotrophic CO_2 production estimate was based on measurements taken between 30 and 80 days after the installation of the collars and severing the roots, as this was a period of stable ratios of the deep to shallow collar effluxes (McElligott et al., 2016; Templeton et al., 2015). The 48 collar pairs at each site were measured over the course of a year on five to eight separate campaigns during 1 year at each site. Total soil CO_2 efflux from the shallow collars was measured for multiple years, during 2012–2015.

Soil temperature (*T*s) was measured continuously throughout the study (2012–2015) in triplicate in each treatment plot using CWS655 probes (Campbell Scientific, USA), and were used to produce continuous R_S time series for each plot based on the empirical relationships between observed R_S and simultaneous manual measurements of *T*s (Bracho et al., 2018). Annual R_{SH} fluxes were estimated by multiplying the plot-level R_S estimates with the plot-level mean R_{SH}:R_S ratio. This approach did not differ from estimates where the smaller number of R_{SH} measurements were scaled directly with *Ts* (Bracho et al., 2018). R_{SA} was estimated as the difference between plot-level R_S and R_{SH}, and net ecosystem productivity (NEP) was estimated as the difference between TNPP and R_{SH}.

2.3. Statistical Analysis

The global treatment effects of throughfall exclusion and fertilization on carbon fluxes were analyzed based on annually integrated fluxes. The sample size for the statistical analysis was 192 (3 sites × 4 treatments × 4 replicates × 4 years). The year was used as a repeated measure, site as a random factor, and the fertilization and drought treatments were the main effects. The main and interactive effects of drought and fertilization were determined with repeated measures ANOVA using the Kenward-Roger method for calculating the denominator degrees of freedom to account for the small sample size (PROC MIXED, SAS v 9.4, SAS Institute). Site differences were estimated with site, D and F as interacting main effects, and year as a repeated measure. The significance of site and treatment differences was estimated with Tukey's honestly significant difference (HSD) test at $\alpha < 0.05$ level. Marginally significant effects at $0.05 < \alpha < 0.1$ are noted individually. The site-by-treatment interactions were not statistically significant, allowing us to summarize global treatment effects across the study domain. Compared to the site-specific analysis (Bracho et al., 2018), the current study has one fewer study site. Data from GA were excluded from the current analysis because of deviations in R_{SH} measurement protocol at that site.

3. Results and Discussion

Despite large latitudinal differences in productivity and respiration fluxes, the three study sites spanning the native range of the species (6.5°C in MAT and 300 mm in MAP) exhibited universal patterns in the divergence of NPP and NEP to the drought and fertilization treatments. Plant productivity (TNPP) and heterotrophic soil CO_2 efflux (R_{SH}) were greater in FL than in OK and VA (Figure 2a, 2c, and 2e), whereas the autotrophic soil CO_2 efflux was similar and higher in FL and OK than VA (Figure 2g). Accounting for the site differences, the responses to drought and fertilization treatments were consistent across locations during the 4-year study period (Figures 2b, 2d, 2f, and 2h, Table 2), even though the magnitude and timing varied (Bracho et al., 2018). The nearly twofold regional differences, and treatment responses to drought and fertilization in total and belowground net primary production (TNPP and BNPP) were reflected in opposite changes in the heterotrophic soil CO_2 efflux (R_{SH}), possibly mediated by the fresh carbohydrate control of exudation and soil microbial activity (Meier et al., 2017; Mitra et al., 2019). Fertilization increased productivity (TNPP: +9%, $p = 0.0005$; BNPP: +12%, $p = 0.0003$), and decreased R_{SA} (−12%, $p = 0.068$) and R_{SH} (−7%, $p = 0.0024$). At the individual site level (Bracho et al., 2018), fertilization effects on TNPP were significant

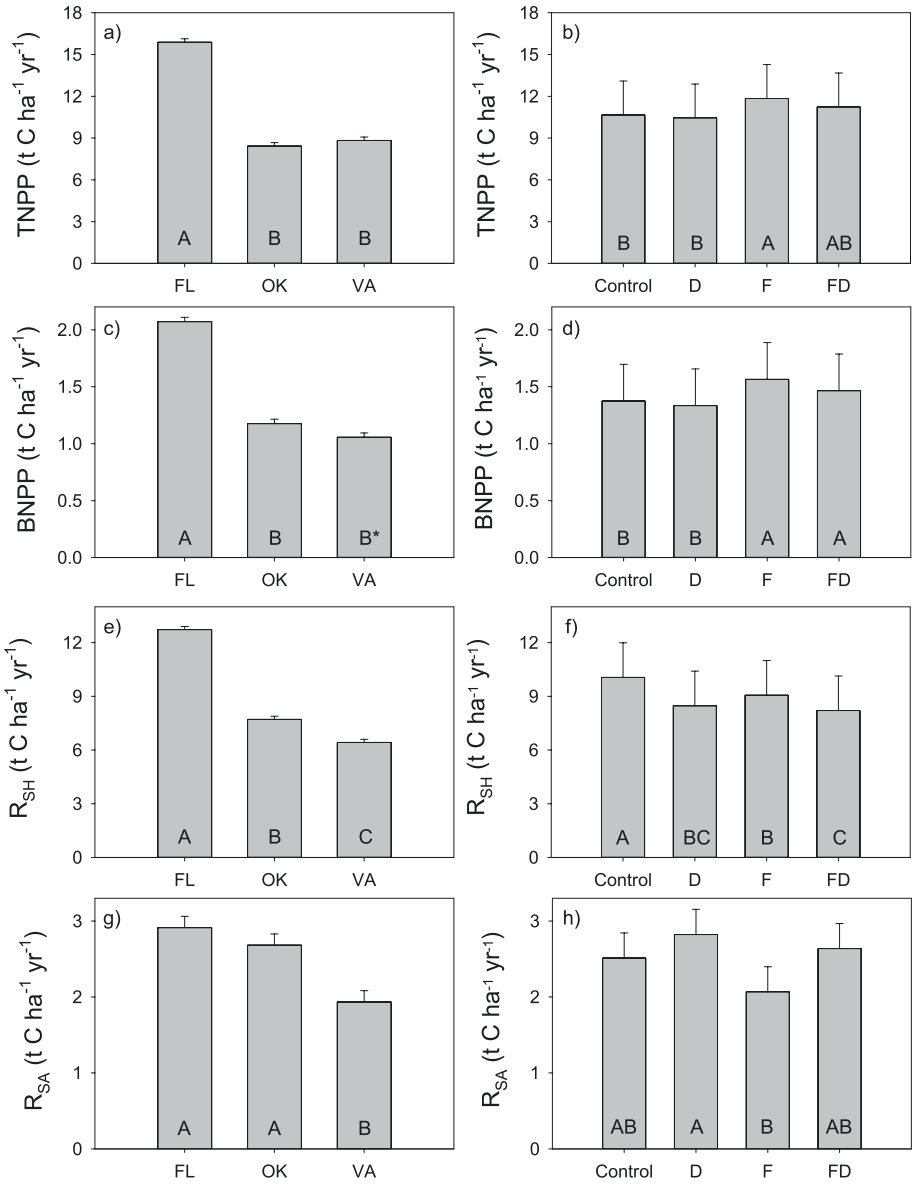

Figure 2. Four-year weighted mean annual fluxes by site (left column; weighted mean ± SE) and by experimental treatment (right)—total net primary production (TNPP; a, b), belowground net primary production (BNPP; c, d), soil heterotrophic CO_2 efflux (R_{SH}; e, f), and soil autotrophic CO_2 efflux (R_{SA}; g, h). All values are repeated measures weighted mean ± SE). The letters indicate Tukey's HSD post-hoc comparisons between treatments—different letters indicate statistically significant difference at $\alpha < 0.05$ level. The asterisk indicates a difference from categories with the same letter at $\alpha < 0.1$ level (BNPP). The significance of main treatment effects is shown in Table 2.

at all sites ($p < 0.005$), with no interaction with drought treatment, but with significant year by fertilization interaction at the OK site—the fertilization effect disappeared by the fourth year of measurement. R_{SH} responses to fertilization were statistically significant at OK and VA, but not in FL (Bracho et al., 2018). In the current analysis, with site as a random factor, R_{SH} decreased significantly in response to fertilization (both in absolute and normalized scale; Table 2; Figures 2f and 3f), leading to much greater proportional increases in NEP than in TNPP (89% vs. 9%; Figures 2b and 3h; Table 2). Drought did not significantly affect productivity in the current cross-site analysis (although at site level, TNPP decreased in OK; Bracho et al., 2018). As the result of a lower heterotrophic fraction of soil CO_2 efflux (R_{SH}:R_S ratio, Figure 3b), drought increased NEP and carbon sequestration efficiency (NEP:NPP; Figure 3h and 3j). The different partitioning of respiratory costs among sites and in response to drought and fertilization treatments led to the divergence between

Table 2
P-Values of Drought (D) and Fertilization (F) Main Effects and Their Interaction Across all Years and Sites for Main Carbon Fluxes and Their Ratios

Flux	Drought	Fertilization	$D \times F$	Ratio	Drought	Fertilization	$D \times F$
TNPP	0.146	0.0005	0.4825	R_{SH}:TNPP	0.0009	<0.0001	0.0823
BNPP	0.1119	0.0003	0.4978	R_{SA}:TNPP	0.0013	0.0048	0.1910
R_{SH}	<0.0001	0.0024	0.0798	R_{SH}:BNPP	0.0027	<0.0001	0.1464
R_{SA}	0.0112	0.0680	0.4497	R_{SA}:BNPP	0.0007	0.0024	0.2231
NEP	0.0218	<0.0001	0.0284	NEP:TNPP	0.0009	<0.0001	0.0823
				R_{SH}:R_S	<0.0001	0.4421	0.2696

Abbreviations: BNPP, belowground net primary production; NEP, net ecosystem production; TNPP, total net primary production.

TNPP and NEP. NEP was comparable in VA and FL, despite their nearly twofold difference in TNPP (Figures 2a and 3g). While TNPP and BNPP increased by about 10% under fertilization, and showed a minimal response to drought treatment, NEP increased in response to both fertilization (threefold) and drought (>2-fold at ambient nutrient availability) across all sites (Figure 3h).

The central role of nutrient status in affecting carbon allocation and various carbon conversion efficiency metrics has been demonstrated in several recent syntheses (Campioli et al., 2015; Fernandez-Martinez et al., 2014; Vicca et al., 2012). Both the biomass production efficiency (BPE=NPP:GPP; Campioli et al., 2015; Vicca et al., 2012) and ecosystem carbon use efficiency (CUE=NEP:GPP; Fernandez-Martinez et al., 2014) are higher in nutrient-rich than nutrient-poor forests. These findings suggest that both R_{SA} and R_{SH} must respond to nutrient availability, but the current study is the first experimental assessment in this regard. The marginally significant decrease of R_{SA} under fertilization (Table 2; Figures 2 and 3) is consistent with the body of evidence that improved nutrient availability shifts allocation from belowground toward aboveground tissues (Chen et al., 2013). However, given that BNPP and TNPP were both derived from fixed allometric equations, direct confirmation of such presumed change is not possible with the current data set. Overall, assuming that autotrophic respiration is 50% of GPP (Waring et al., 1998), the carbon sequestration efficiencies (NEP:TNPP) in Figure 3j convert to CUE of about 0.05 (control), 0.13–0.14 (D & F treatments), and 0.16 (combined treatment), similar to the estimates of Fernandez-Martinez et al. (2014).

Our results are unique in that R_{SA} increased under drought, whereas in most other studies R_{SA} declined instead (Hinko-Najera et al., 2015; Huang et al., 2018; Li et al., 2018; Risk et al., 2012; Sun et al., 2019). We attribute this to the more moderate treatment design (−30% throughfall exclusion in the current study vs. −40%, −50%, or even −100% seasonal exclusion in others), and unusually high precipitation in the second and third year of the current study (Bracho et al., 2018; Will et al., 2015), which likely ameliorated any physiological drought responses. The slight increase in R_{SA} under drought suggests that the effect was barely strong enough to trigger enhanced root growth and increased exploration of soil volume (Ward et al., 2015). On the other hand, the small (−7%) but universal decline in R_{SH}, especially when normalized for BNPP (−19%; Figure 3f), that was consistent across sites, is a response that has not been described in most earlier studies. The results of Siebert et al. (2019) indicate that this may be due to the differential responses of soil invertebrates (more sensitive) and microbes (less sensitive) to soil moisture. In some studies, drought plots have had higher temperature, which may have compensated for the negative effects of lower moisture on R_{SH} (Schindlbacher et al., 2012), but in the current study, soil temperature did not differ between the water availability treatments (data not shown). Thus, the observed differences in R_{SH} in the current study are solely in response to soil moisture.

The progressive decline in R_{SH} in proportion to BNPP (Figure 3f) from single to combined treatments suggests active control by plants of carbohydrate exudation to the soil environment based on resource availability. The drought treatment would have reduced plant carbohydrate status while increasing sink strength, whereas the fertilization treatment increased nutrient availability for plants, and made them less dependent on rhizosymbionts for nutrient mineralization. Both aspects are consistent with the idea of tight coupling between plant nutrient demand, and energy limitation of the decomposer community (Averill &

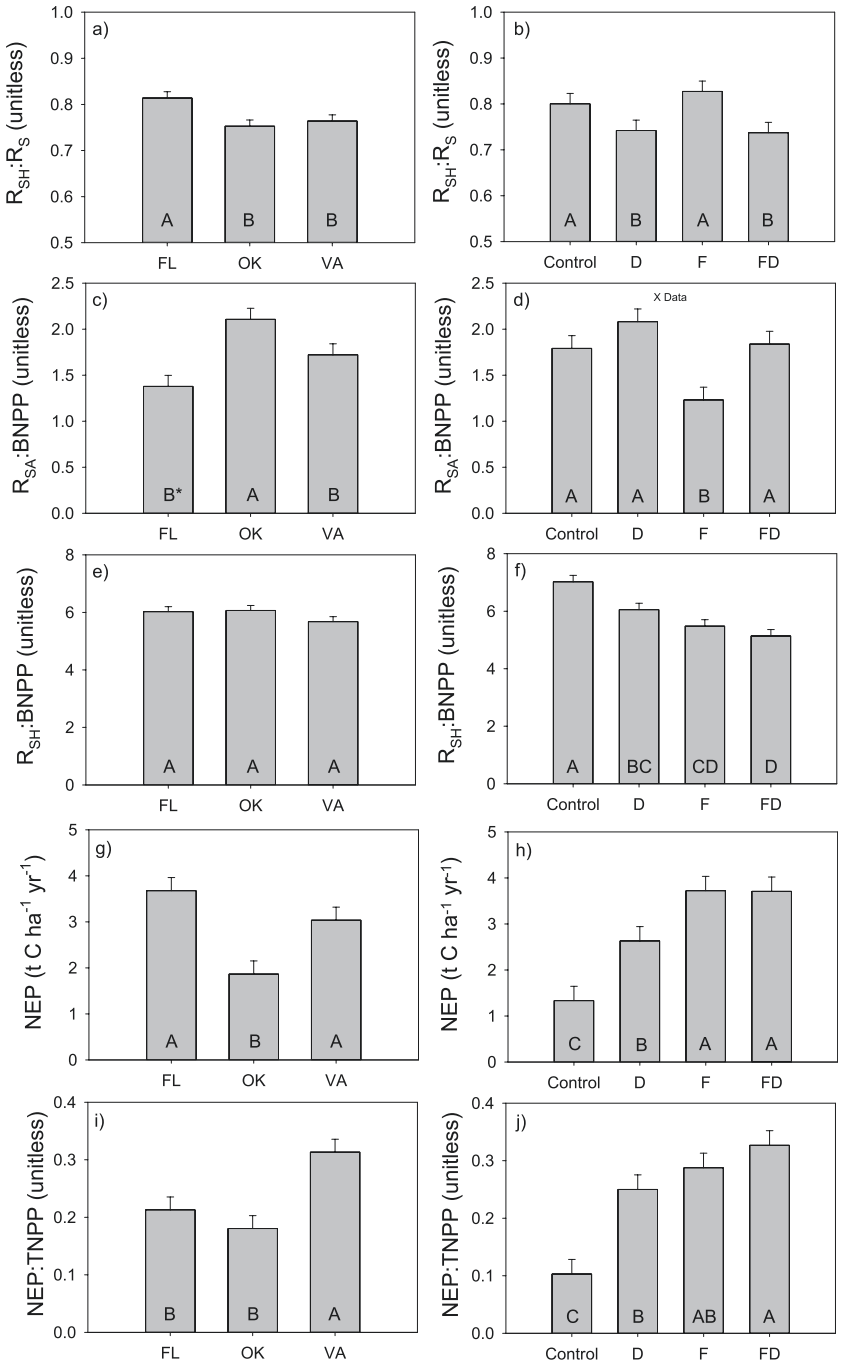

Figure 3. The ratio of soil heterotrophic respiration to total soil CO_2 efflux (R_{SH}:R_S; a, b), ratio of R_{SA} to belowground productivity (R_{SA}:BNPP; c, d), ratio of soil heterotrophic respiration to BNPP (R_{SH}:BNPP; e, f), net ecosystem production (NEP; g, h) and carbon sequestration efficiency (NEP:TNPP ratio; i, j) across sites (left column) and among treatments (right column). All values are repeated measures weighted means ± SE. The letters indicate Tukey's HSD post-hoc comparisons between treatments—different letters indicate statistically significant difference at $\alpha < 0.05$ level. The asterisk indicates a difference from categories with the same letter at $\alpha < 0.1$ level (R_{SA}:BNPP). The significance of main treatment effects is shown in Table 2.

Waring, 2018; Mitra et al., 2019) that use fresh plant-derived carbohydrates to "prime" the decomposition of more complex organic molecules (Kuzyakov, 2010). The additive sensitivity of R_{SH} to drought and fertilization explains the increased carbon sequestration efficiency (Figure 3j), and the change in the ranking of sites by NEP compared to TNPP (Figures 2a, 3g and 3h).

The observed divergence of TNPP and NEP responses to water and nutrient availability have far-reaching implications for (1) modeling of ecosystem carbon fluxes, (2) projections of ecosystems' capacity to mitigate climate change, and (3) the profitability of forest production when timber income and carbon sequestration benefits are considered together. Although the current study was conducted in simple-structured managed plantation forests, the principles of resource-availability-driven patterns of allocation and plant-microbe interactions are universal and apply to all ecosystems. Therefore, we conclude that the results of this study can be used to validate ecosystem and land surface models. Given that R_{SH} is among the most poorly constrained fluxes in the carbon cycle and a universally recognized weakness in land surface models (Lawrence et al., 2019; Wieder et al., 2019), improved understanding and more realistic representation of this process in models deserves renewed focus. Increasing anthropogenic nutrient inputs through fertilization, agricultural runoff, and atmospheric deposition are worldwide, and this increase in resource availability affects mycorrhizal and other symbiotic relationships formed by plants (Meier et al., 2017), which, in turn, manifest in carbon allocation patterns (Litton et al., 2007; Waring et al., 2010), detritus production pathways, and carbon sequestration efficiency. For climate mitigation, ecosystems' value is, in part, measured by their ability to sequester carbon in long-lived pools, which is equal to long-term average NEP, accounting for episodic disturbances and removals (also called net biome production, NBP). Given that the higher frequency of droughts projected for the coming decades might manifest primarily through higher atmospheric evaporative demand (Novick et al., 2016), the NEP gain under mild drought suggested by the current study is a significant benefit, especially as the TNPP cost of the drought was minimal. Notably, the NEP benefit was greater at lower nutrient availability (as is expected in extensively managed public- and small landowner-owned forests). On the other hand, realizing this potential may be hampered by longer and more severe droughts that can reduce both TNPP and NEP (Bracho et al., 2012; Schwalm et al., 2012; Yang et al., 2018), and by elevated R_{SH} under excessive soil disturbance in intensively managed production forests (Noormets et al., 2015). Finally, if forests become valued not only for their harvestable timber production but also for their carbon sequestration potential (https://ecosystemservicesmarket.org/), less productive sites on nutrient-poor and marginal lands may exhibit similar NEP to more productive sites due to lower R_{SH}, and thus offer the landowners an alternative revenue source.

Data Availability Statement

All data are archived at and available from the Terra-C database at the University of Florida (http://terrac.ifas.ufl.edu/index.asp).

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