



Respiratory Acclimation of Tropical Forest Roots in Response to In Situ Experimental Warming and Hurricane Disturbance

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ABSTRACT

Climate projections predict higher temperatures and more frequent hurricanes in the tropics. Tropical plants subjected to these stresses may respond by acclimating their physiology. We investigated tropical forest root respiration in response to in situ experimental warming and hurricane disturbance in eastern Puerto Rico. We measured mass-normalized root specific respiration, root biomass, and root traits at the Tropical Responses to Altered Climate Experiment (TRACE), where understory vegetation is warmed + 4 °C above ambient. Our measurements span 5 years, including before and after two major hurricanes, to quantify root contributions to ecosystem carbon fluxes. Experimental warming did not affect root specific respiration at a standard temperature of 25° (RSR₂₅, mean = 3.89 nmol CO₂ g⁻¹ s⁻¹) or the temperature sensitivity of root respiration (Q₁₀, mean = 1.75), but did result in decreased fine-root biomass, thereby decreasing area-based estimations of ecosystem-level root respiration in warmed plots

by ~ 35%. RSR₂₅ of newer roots, which increased with increasing root nitrogen, showed greater rates 6 months after the hurricanes, but subsequently decreased after 12 months. Root specific respiration did not acclimate to higher temperatures, based on lack of adjustments in either Q₁₀ or RSR₂₅ in the warmed plots; however, decreased root biomass indicates the root contribution to soil carbon dioxide efflux was overall lower with warming. Lower root biomass may also limit nutrient and water uptake, having potential negative effects on carbon assimilation. Our results show that warming and hurricane disturbance have strong potential to affect tropical forest roots, as well as ecosystem carbon fluxes.

Key words: acclimation; climate change; disturbance; experimental warming; root respiration; tropical plants; TRACE.

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HIGHLIGHTS

- Tropical forest mass-based root respiration did not respond to experimental warming
- Area-based ecosystem root respiration decreased

with warming via lower root biomass

- Root specific respiration increased following hurricanes then declined after a year

INTRODUCTION

Tropical forests exchange more carbon with the atmosphere than any other category of ecosystem, and tropical soils represent about 30% of soil organic carbon, globally (Jobbagy and Jackson 2000; Tarnocai and others 2009). Both ongoing and predicted climate change have the potential to dramatically alter tropical forest carbon stocks and fluxes. For example, with higher projected global atmospheric temperatures (IPCC 2018) and increased frequency and intensity of tropical cyclone disturbances (Knutson and others 2019), tropical plants will face environmental stresses that could alter how they use carbon for energy. This would have implications not only for carbon fluxes aboveground, but also for belowground carbon cycling, including in roots. Root respiration is estimated to account for 30–50% of total soil carbon dioxide (CO₂) efflux (Bond-Lamberty and others 2004), but is rarely explicitly measured in carbon flux studies; thus anthropogenic effects on roots may represent a large and poorly quantified feedback to global change.

Plant respiration is a temperature-sensitive process that increases exponentially with increasing measurement temperatures as enzymatic metabolism increases (Atkin and Tjoelker 2003). In response to short-term or long-term exposure to warmer growth temperatures, root respiration can acclimate, or change to accommodate new climate conditions, by either down-regulating respiratory basal rates (for example, RSR₂₅; mass-based root specific respiration rate at 25 °C) or reducing respiratory temperature sensitivity (for example, Q₁₀; rate of respiration change over a 10 °C change in temperature) to use carbon stores more efficiently at higher temperatures (Atkin and Tjoelker 2003). As such, with increased temperatures root respiration acclimation responses could mitigate total contributions to global soil CO₂ efflux, thereby decreasing the strength of the reinforcing feedback between respiratory CO₂ emissions and global warming (Tjoelker 2018). While the signal accuracy of carbon flux responses to warming in Earth System Models (ESMs) is improving, the role of tropical ecosystems in terrestrial carbon exchange is highly variable in those models (Cavaleri and others 2015). Understanding the broad spectrum of root structural and functional responses, including

respiration, to increased temperature will inform ESMs to better estimate future biogeochemical cycling (Warren and others 2015).

Soil CO₂ efflux is primarily the respiratory byproduct of invertebrates, bacteria, fungi, and roots. Soil organisms may have different magnitudes of respiration response to higher temperatures, and parameterizing how heterotrophs and autotrophs differ in response to warming will both improve representation of soil CO₂ efflux in ESMs and also enhance our understanding of ecosystem function (Subke and Bahn 2010; Hopkins and others 2013). Root respiration can be parameterized within ESMs with temperature-dependent values of basal metabolism (for example, RSR₂₅) or temperature sensitivity (for example, Q₁₀). RSR₂₅ and Q₁₀ are modeled parameters derived from measuring respiration rates at different temperatures, and thermal acclimation can be characterized by a decrease in either parameter under higher growth temperatures (Atkin and Tjoelker 2003).

Ecosystems subjected to frequent disturbances can generate a “resilience debt”, which is when aspects of ecosystem function are no longer sustained due to increasing frequency of disturbance (Johnstone and others 2016). Our study site, the Tropical Responses to Altered Climate Experiment (TRACE), a tropical wet forest understory and soil warming experiment, was hit by two major hurricanes in 2017 that knocked down much of the canopy causing a “pulse” disturbance on top of the “press” disturbance from our experimental warming. Tropical cyclones (also called hurricanes and typhoons depending on location) can reduce root biomass in the long-term even though root growth rates can increase within months following hurricane disturbance and then significantly decrease below pre-hurricane levels after 6 months (Silver and Vogt 1993). For example, 10 months after a hurricane disturbance at the TRACE site, Yaffar and others (2021) found root biomass increased 2.8-fold in the control (unwarmed) plots, but increased only 1.6-fold in roots exposed to a year of experimental warming before the disturbance. This reduction in biomass production in previously warmed plots relative to control plots persisted for nearly a full year, despite no active warming during this timeframe. These results suggest a legacy effect of warming may have contributed to the “resilience debt” accrued through both pulse (for example, hurricanes) and press (for example, chronic warming) disturbances. Slower root regrowth in experimentally warmed plots after hurricanes also suggests there is the potential for a smaller root contribution to total soil CO₂ efflux

following hurricanes in a warmer climate, if root specific respiration rates remain unchanged or heterotrophic soil respiration rates increase with warming (for example, Wood and others unpublished).

Very few studies have evaluated temperature effects on root respiration of tropical species. A greenhouse study of Australian tropical tree seedlings found evidence of root specific respiration acclimation in response to experimental warming for only one of eight species studied (Noh and others 2020). An in situ experimental soil warming study in a Panamanian tropical forest which used root exclusion methods and soil CO₂ efflux partitioning found no evidence of root thermal acclimation (Nottingham and others 2020). However, to our knowledge, there are no studies directly measuring root specific respiration response to warming in situ, nor any studies showing the interacting effects of long-term warming and hurricane disturbance on tropical root respiration.

Similar to the leaf economic spectrum, where acquisitive leaf traits are associated with short-lived leaves and conservative traits are associated with long-lived leaves (for example, Wright and others 2004), roots exhibit a similar economic spectrum, where acquisitive roots have higher root specific respiration rates (RSR, nmol CO₂ g⁻¹ s⁻¹), nitrogen concentrations (N_{root} , %), specific root length (SRL, cm g⁻¹), and lower root tissue density (RTD, g cm⁻³) than conservative roots (Roumet and others 2016). Root morphological traits have been found to change in tropical seedlings when experimentally warmed by increasing both SRL and N_{root} and decreasing RTD (Noh and others 2020). These responses to warming are characteristic of roots with nutrient acquisitive strategies, and they usually result in higher respiration rates (Roumet and others 2016). Trait responses to warming can be species-specific, but the amount of variation in morphological traits that affect root respiration can be nearly as high within a plant as among plants within the ecosystem (Paradiso and others 2019). Overall, roots in the TRACE site became longer per unit mass (that is, greater SRL) after the hurricanes in Puerto Rico, (Yaffar and others 2021), suggesting some plants may have switched to a more acquisitive strategy after the disturbance, or the signal may be indicative of a shift in community composition towards more acquisitive species (Kennard and others 2020).

Here, we sought to take advantage of a unique opportunity to assess the effects of warming and hurricane disturbance on root biomass, respiration, acclimation, and traits. We hypothesized that (H1)

long-term in situ experimental warming would not induce acclimation (that is, down-regulation) of root specific respiration, and that post-hurricane root specific respiration would increase in warmed plots to compensate for lower root mass and/or pulses of available soil nutrients. We also hypothesized that (H2) ecosystem root respiration at 25 °C (scaled up per unit area using root biomass and root specific respiration rates in the top 10 cm of soil) before the hurricanes would be lower in warmed plots than control plots because of reduced root biomass under warming. Furthermore, we hypothesized that this trend would continue after the hurricanes even when plots were not warmed due to legacy effects of the warming treatment. Finally, we hypothesized that (H3) roots would move towards a more acquisitive strategy for nutrient uptake in warmed plots and after the hurricanes through increased N_{root} and SRL, and decreased root tissue density, traits which are associated with higher rates of root specific respiration.

MATERIALS AND METHODS

Site Description

This study was conducted from 2017 to 2020 at the Tropical Responses to Altered Climate Experiment (TRACE), a subtropical wet forest understory and soil warming experiment located in the Luquillo Experimental Forest in Puerto Rico (18.32465° N, 65.73058° W). Mean annual temperature at the site is 24 °C (Kimball and others 2018) and mean annual precipitation is ~ 3500 mm (Murphy and others 2017). Acidic, red clay soils at the TRACE site are classified as Ultisols (Scatena 1989). The TRACE project consists of three ambient temperature (that is, control) and three experimentally warmed plots, each hexagonally shaped with 4 m diameter. Experimental plots were warmed 4 °C above the average surface temperature of the control plot temperatures using infrared (IR) heaters 1–2 m above the vegetation (Kimball and others 2018). Initially after the hurricanes, the heaters were at about 2.5 m above the ground and were moved to their max height of 4 m in July 2020 as the understory vegetation height increased. Each plot had similar composition of understory plant species and were mainly composed of *Psychotria brachiata*, *Piper glabrescens*, *Guarea guidonia*, *Miconia racemosa*, *Inga vera*, and *Prestoea acuminata*.

In September 2017, two major hurricanes made landfall on Puerto Rico, causing heavy disturbance of the forest canopy and severely damaging the

electrical infrastructure of the island. The TRACE warming infrastructure was repaired by July 2018, and experimental warming was restarted on September 28, 2018 after one year of post-hurricane baseline data collection without warming under new canopy conditions. There was a successional shift in plant species diversity within a year after the hurricanes, during which there was a large population of grasses in the understory (Kennard and others 2020). Grasses and herbaceous plants were shaded out by the early successional tree *Cecropia schreberiana*, which had not been in the plots previously, within two years after the hurricanes (unpublished data). Over the course of the experiment, warming was started in September 2016, paused for a year after the hurricanes in September 2017, and restarted in September 2018, and warming has been continuous to date, except for periodic maintenance. Prior to the hurricanes, surface soils (0–10 cm; where most of the roots are located) were warmed + 3.6 °C over control soils, and an average of ~ + 3 °C warming effect was observed at soil depths up to 50 cm (Kimball and others 2018). After the hurricanes, however, higher understory foliage density caused the warming effect in the upper 10 cm of soil to be reduced to ~ + 1 °C (Figure 1), and negligible warming was detected in the deeper soils.

Experimental Design

For each root specific respiration campaign, we took 3 plot replicate cores for each of the 6 plots, totaling 18 cores per campaign and 9 cores per treatment. Each sampling day, from 8:00 to 17:00 AST, one core from each plot was removed and sampled in a randomized order. Cores were weighed, roots were separated from soil, and soil-free roots were measured for respiration. Two dif-

ferent types of root cores were removed from the plots: fresh bulk soil cores and root ingrowth cores. Fresh cores were taken by driving a 5.08 cm diameter PVC pipe into the first 10 cm of undisturbed soil. Root ingrowth cores were 10 cm deep, 5.08 cm diameter plastic tubes with 1.5 mm mesh that were placed in the hole left when each fresh core was taken. Root ingrowth cores were filled with 275 g homogenized root-free soil taken from a 10 cm -deep soil pit located just outside of the study area, which is based on mean bulk density of soils for the site (Yaffar and others 2021). Distinction between these cores is important because roots in a root ingrowth core represent newer growth that may have higher respiration rates due to higher enzymatic activity associated with potentially higher metabolic demand required for growth, and due to differences in soil structure between the two methods. Fresh cores were collected in March 2017, March 2018, September 2018, and March 2019 and root ingrowth cores were collected in July 2017, March 2018, July 2018, September 2018, March 2019, November 2019, March 2020, and October 2020.

Environmental Data

Hourly measurements of soil temperature and moisture in the first 10 cm was averaged among the three surface soil temperature/moisture probes (CS655, Campbell Scientific, Logan, UT) located at the edge, midway to the center, and center of each plot and then averaged over the 10 days before cores were extracted. Deeper soil temperature and moisture (20–30 cm and 40–50 cm) data were not used in this study because the focal roots were only 0–10 cm deep. Hourly vegetation temperature measured using IR thermometers (SI-121, Apogee Instruments, Logan, UT) was averaged over the 10 days before cores were extracted.

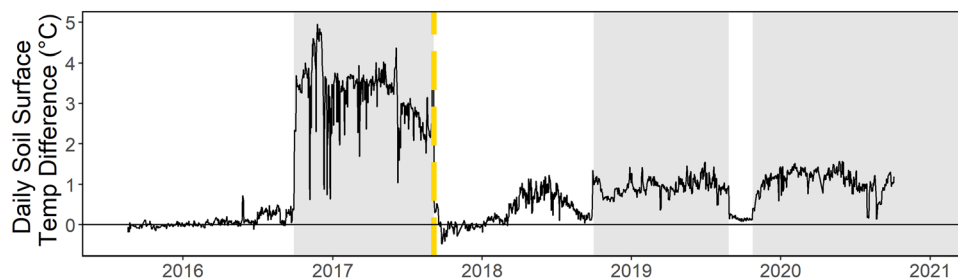


Figure 1. Daily difference between the means of soil temperature in the upper 10 cm of soil for warmed and control plots. Shaded blocks show where warming was turned on and white blocks show where warming was not turned on. Hurricanes occurred at dashed yellow lines.

Respiration Measurements

Root specific respiration measurements ($\text{nmol CO}_2 \text{ g}^{-1} \text{ root s}^{-1}$) were taken on soil-free fine roots ($< 2 \text{ mm}$ diameter) picked from the cores for 20 total person-minutes (two people $\times 10 \text{ min}$ of picking). This timing was selected to minimize a decay in respiration rates before the roots were measured. After the first 10 min, the remaining roots were separated from the soil to measure total fine root biomass per core. Respiration was measured by placing soil-free roots in a 0.116 L aluminum cuvette equipped with a type-T temperature probe in a closed loop system in-line with a CA-10 infrared gas analyzer (IRGA; Sable System, North Las Vegas, NV, USA) and a Sable System SS-4 subsampling pump totaling 0.186 L of system volume. Data were collected from the system using a Sable System UI-3 connected to a computer with Sable Systems Expedata software. Flow rate for the system was set to 400 ml min^{-1} with the Sable Systems SS-4. Data collection was initiated when the system was at stable temperature, and $\% \text{CO}_2$ and air temperature within the cuvette were measured for 5 min using Expedata software. Respiration rates were measured at three different temperatures (23, 25, and 30°C) to generate a temperature response curve from which temperature sensitivity parameters were extracted. Root respiration was initially measured at 25°C for each core and then measured at either 23°C or 30°C before finally being measured at the remaining temperature of 23°C or 30°C . Root temperature was controlled by placing root cuvettes in insulated lunchbox coolers filled with water near the target temperatures. Air temperature within the cuvette was controlled with addition of hot water or ice to the water bath to heat or cool the cuvette air, respectively. Following each measurement, roots were removed from the cuvette and placed in the next cuvette at the following temperature in the sequence. All respiration measurements were taken within an hour of the soil cores being removed from the plots.

Respiration rate was converted from $\Delta\% \text{CO}_2 \text{ s}^{-1}$ to $\text{nmol CO}_2 \text{ s}^{-1}$ by multiplying $\Delta\% \text{CO}_2 \text{ s}^{-1}$ by the nmol of air in the system, which was calculated as follows:

$$\text{nmol CO}_2 \text{ s}^{-1} = \Delta\% \text{CO}_2 \text{ s}^{-1} * \left(\frac{PV}{RT} \right) * 10^{-9} \text{ nmol mol}^{-1} \quad (1)$$

where P is pressure (atm), V is system volume (L), T is measurement temperature (K), and R is the ideal gas constant ($0.0821 \text{ atm L mol}^{-1} \text{ K}^{-1}$). Root

specific respiration ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$) was calculated as the respiration rate divided by the dry mass of roots used in the measurement. Within the hour when roots are being measured, root respiration rate decays, therefore a correction factor was applied to respiration response. Corrected respiration rate (CRR ; $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$) was calculated as follows:

$$\text{CRR} = \text{RR} + t * c \quad (2)$$

where RR is measured respiration rate ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$), t is seconds since roots were extracted from ground (s), and c is a coefficient of $0.6107 \text{ (nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1})$. The correction coefficient was calculated in a pilot study by repeating measurements on several sets of roots at the same temperature over two hours during which respiration rate decayed (data not shown).

Root specific respiration temperature response parameters were calculated by fitting CRR values from each core to a curve using a non-linear least squares regression with the 'nls' function in R statistical language (R Core Team 2020) with the equation below:

$$\text{CRR} = \beta_0 * e^{\beta_1 T} \quad (3)$$

where T is measurement temperature and β_0 and β_1 are modeled parameters used for extracting RSR_{25} and Q_{10} . For each temperature curve, Q_{10} (unitless) was calculated using the equation:

$$Q_{10} = e^{\beta_1 * 10} \quad (4)$$

and RSR_{25} ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$) was calculated using the equation:

$$\text{RSR}_{25} = \beta_0 * e^{\beta_1 * 25} \quad (5)$$

Area-based estimations of root specific respiration (ecosystem root respiration, $\text{g m}^{-2} \text{ d}^{-1}$), were scaled up from root biomass per unit ground surface area of 10 cm deep cores. Ecosystem root respiration at 25°C was calculated as:

$$\text{Ecosystem root respiration} = \frac{\text{biomass}}{A} * \text{RSR}_{25} \quad (6)$$

where biomass is the core total fine root biomass (g), and A is the area of the upper surface of each core ($2.0268 \times 10^{-3} \text{ m}^2$).

Root Trait Measurements and Soil Nutrients

After respiration measurements, living roots were sorted from dead roots, imaged with an EPSON Perfection V800 Scanner containing an acrylic tray

filled with DI water, and analyzed for root length, diameter, surface area, and volume using WinRHIZO software (Regent Instruments Inc., Quebec, Canada) to calculate specific root length (cm g^{-1}), mean diameter (mm), and root tissue density (g cm^{-3}). Living and dead roots were dried separately at 65 °C for 48 h and weighed to determine total dry biomass.

Roots were measured for percent carbon and nitrogen, and soil from the collection cores was subsampled for soil ammonium (NH_4^+ , $\mu\text{g g dry soil}^{-1}$), nitrate (NO_3^- , $\mu\text{g g dry soil}^{-1}$), and extractable phosphate (PO_4^{3-} , $\mu\text{g g dry soil}^{-1}$). Dried roots used for respiration and morphological trait measurements were ground in a ball-mill (SPEX 8000D, SPEX Sample Prep, Metuchen, NJ, USA) and analyzed for percent carbon and nitrogen on an elemental analyzer (Elementar Vario Micro Cube, Elementar Inc., Langenelsbold, Germany). Core soil extractable NH_4^+ and NO_3^- were assessed on fresh soils the same day as collection by extracting soil with 2 N KCl by shaking for 1 h, allowing extracts to sit overnight, filtering through Whatman #1 filter paper (GE Healthcare, Chicago, IL), freezing immediately, and storing frozen until analysis (based on (Robertson and others 1999) as described in (Reed and others 2008)). Extracts were measured using an indophenol blue and cadmium reduction colorimetric assay on a discrete analyzer (Unity Scientific Smartchem 200 Discrete autoanalyzer, Milford, MA). Soil Bray-extractable PO_4^{3-} was extracted by shaking fresh soil with Bray solution (dilute HCl and NH_4F) for 1 min (Bray and Kurtz 1945). Bray extractions were filtered through Whatman #1 filter paper, frozen, and stored frozen until analysis. Extracts were measured with an ascorbic acid molybdate colorimetric analysis on a SmartChem 200 Discrete Analyzer. All extracts were shipped frozen from Puerto Rico to an analytical chemistry laboratory in Moab, UT (US Geological Survey Southwest Biological Science Center).

Statistical Analyses

Root specific respiration temperature curve parameters (RSR_{25} , Q_{10}), root biomass per unit ground area, ecosystem root respiration, and specific root length relationships with warming treatment effect and hurricane effects were analyzed separately for root ingrowth and fresh cores using two-way ANOVAs, where sampling campaign was used as a time proxy for hurricane effect. Post-hoc Tukey HSD tests were used to determine individual relationships when there was statistical

significance in ANOVAs. RSR_{25} relationships with root trait measurements (specific root length, root tissue density, N_{root} , root mean diameter) and soil nutrients (NH_4^+ , NO_3^- , PO_4^{3-}) for root ingrowth versus fresh core measurements were analyzed with linear models that had the independent variable and core type as interacting variables. All statistical analyses were performed using base R 4.1.2 (R Core Team 2022).

RESULTS

Root Specific Respiration

Root specific respiration did not acclimate in response to experimental warming through down regulation of RSR_{25} or Q_{10} . We did, however, find evidence that root specific respiration in ingrowth cores increased immediately following hurricane disturbance effect, then returned to pre-hurricane rates. There were no significant differences in RSR_{25} or Q_{10} between control and warmed plots, indicating there was no treatment effect before the hurricanes with warming turned on, no legacy effect from warming during regrowth with warming turned off, and no treatment effect during regrowth with warming turned on following hurricane disturbance (Figure 2 Table 1). Q_{10} was not different across campaigns for either core type (Figure 2b); however, there were differences in RSR_{25} between sampling campaigns following the hurricanes for roots in root ingrowth cores, which had higher RSR_{25} in March 2018 than in September 2018 (Figure 2a; Table 1). RSR_{25} did not correlate with plot vegetation temperature, soil surface temperature, or soil surface volumetric water content (Table 2), suggesting the root specific respiration at our site was independent from seasonality of temperature and precipitation. Furthermore, a lack of soil temperature effect on RSR_{25} is support that there is no thermal acclimation of RSR_{25} at our site.

Fine Root Biomass and Ecosystem Root Respiration

While root specific respiration showed no treatment effect, both fine root biomass in the upper 10 cm and ecosystem root respiration at a standard temperature of 25 °C (that is, fine root respiration per unit ground area in the upper 10 cm), showed statistically significant responses to the experimental warming treatment in the fresh cores. Ingrowth cores showed no effect of either treatment or campaign on root biomass or ecosystem root respiration (Figure 3, Table 1). In the fresh cores,

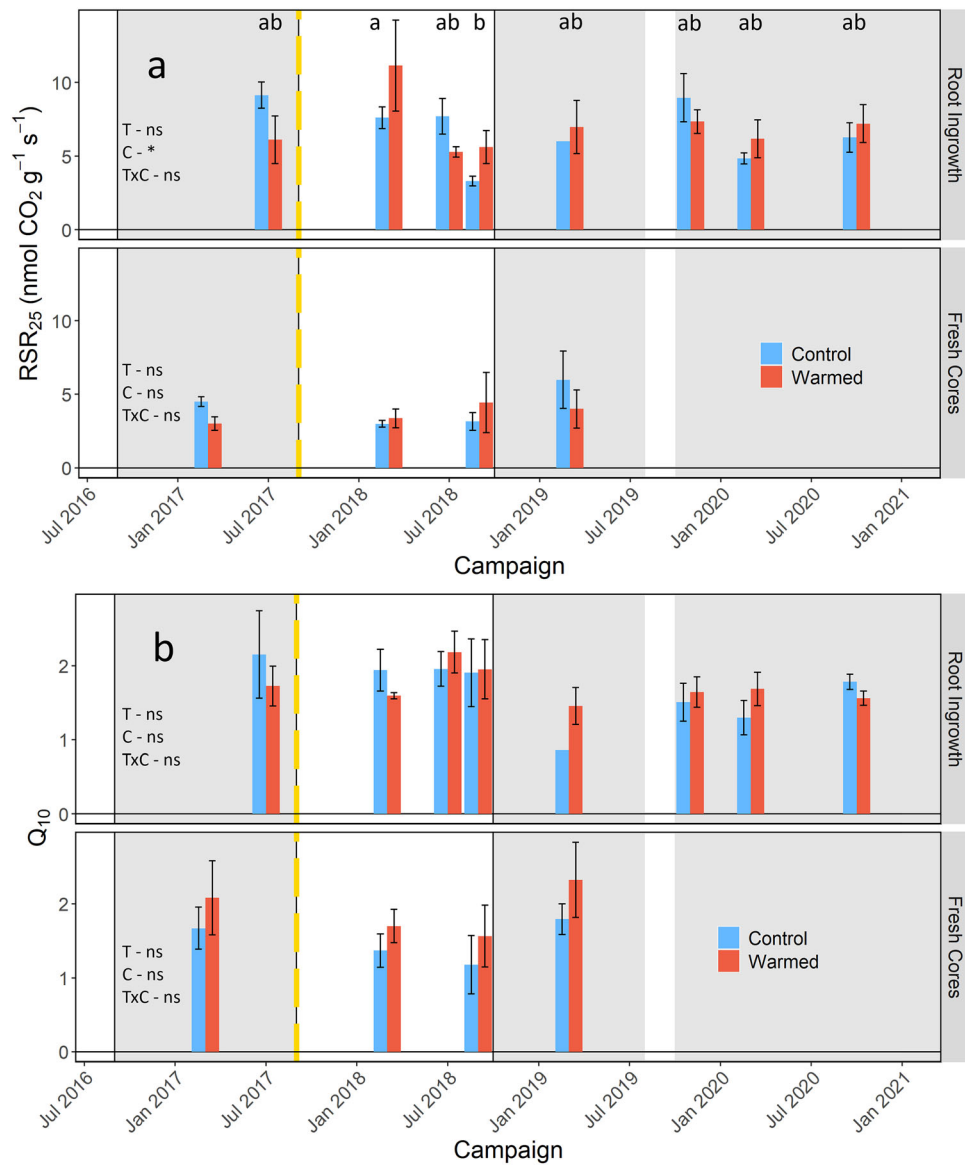


Figure 2. RSR₂₅ (**a**) and Q₁₀ (**b**) for control and warmed plots during each sampling campaign. Root ingrowth campaigns are in the top panel and fresh core campaigns are in the bottom panel for each plot. Shaded blocks show where warming was turned on and white blocks show where warming was not turned on. Hurricanes occurred at dashed yellow lines. The legend in the bottom left shows where there is statistical significance for treatment (T), campaign (C), and treatment x campaign interaction (Tx C) in an ANCOVA. Characters indicate statistical significance between campaigns.

however, root biomass was lower in warmed plots than control plots, even post-hurricane when warming was not active, as there were no significant interactions of treatment and sampling campaign (Figure 3a, Table 1). Ecosystem root respiration of fresh cores showed a marginally significant interaction between treatment and campaign, where rates were lower in warmed plots

compared to control in the pre-hurricane campaign only (Figure 3b, Table 1).

Relationships Between Root Specific Respiration, Root Traits, and Soil Nutrients

Root specific respiration correlated with some root traits but not with soil nutrient variables. RSR₂₅ increased with increasing fine root N_{root} in root

Table 1. ANOVA Table for Fresh and Root Ingrowth Cores With Treatment, Campaign, and Their Interaction as Independent Variables

Core type	Factor	RSR ₂₅ (nmol g root ⁻¹ s ⁻¹)		Q ₁₀ (unitless)		Root biomass (g)		Ecosystem root resp (g C g root ⁻¹ d ⁻¹)	
		df	P	df	P	df	P	df	P
Root ingrowth	Treatment	1	0.82	1	0.98	1	0.25	1	0.67
	Campaign	7	0.013	7	0.30	7	0.21	7	0.070
	Treatment:campaign	7	0.12	7	0.83	7	0.39	7	0.23
Fresh cores	Treatment	1	0.29	1	0.14	1	< 0.001	1	< 0.001
	Campaign	3	0.29	3	0.33	3	0.17	3	0.10
	Treatment:campaign	3	0.35	3	0.99	3	0.13	3	0.051

Statistically significant *p* values with $\alpha < 0.05$ are denoted with bold text.

Table 2. Linear Models of RSR₂₅ Response to Root Traits, Soil Chemistry, and Temperature/Soil Moisture

		<i>n</i>	Independent var	Core type	Var:core type
Root traits	<i>N</i> _{root} (%)	125	< 0.001	0.052	< 0.001
	Specific root length (cm g ⁻¹)	123	0.93	0.005	0.92
	Root tissue density (g cm ⁻³)	123	0.002	0.09	0.32
	Root mean diameter (mm)	123	0.25	0.37	0.63
Soil chemistry	Soil PO ₄ ³⁻ (μg g dry soil ⁻¹)	87	0.71	0.005	0.78
	Soil NO ₃ ⁻ (μg g dry soil ⁻¹)	68	0.12	< 0.001	0.25
	Soil NH ₄ ⁺ (μg g dry soil ⁻¹)	75	0.95	< 0.001	0.45
	Soil carbon (%)	73	0.62	0.49	0.83
	Soil nitrogen (%)	73	0.76	0.77	0.95
	Soil C:N	73	0.45	0.35	0.45
	Vegetation temperature (°C)	125	0.18	0.75	0.87
Environmental	Soil Temperature (°C)	125	0.33	0.68	0.44
	Soil moisture (VWC %)	125	0.77	0.73	0.54

Each value is the *p* value with $\alpha < 0.05$ for the RSR₂₅ response to the independent variable in the first column. Core type indicates a difference between root ingrowth and fresh cores and the interaction indicates RSR₂₅ having a differential response to the independent variable between core types.

ingrowth cores but not in fresh cores (Figure 4a, Table 2). RSR₂₅ was not significantly correlated with specific root length (Figure 4b) or root mean diameter (Figure 4c) but was negatively correlated with root tissue density for both types of cores (Figure 4d, Table 2). RSR₂₅ did not correlate with soil PO₄³⁻, NO₃⁻, NH₄⁺, total soil N, total soil C, or soil C:N for either core type (Figure 5, Table 2). SRL increased dramatically for approximately 9 months following the hurricanes and then returned to pre-hurricanes levels within 15 months for both fresh and root ingrowth cores (Figure 6a, Table 3).

DISCUSSION

Root Respiration Response to Warming

Pre-hurricane root specific respiration did not show a down-regulation under the warming treatment through mechanistic shifts in RSR₂₅ or Q₁₀, par-

tially supporting H1 that long-term warming would not induce acclimation of root specific respiration. However, we also predicted that post-hurricane root specific respiration would increase in warmed plots, which did not occur. We expected lower root biomass and higher nutrient pulses in warmed plots to cause higher root specific respiration rates post-hurricane (H1). While we did observe lower root biomass in the warmed plots for fresh cores, and post-hurricane soil nutrient pulses were found to be greater in warmed plots (Reed and others 2020), these trends did not lead to higher metabolic demand for root respiration per unit root mass. Respiratory thermal acclimation is well studied in leaves (Atkin and Tjoelker 2003; Loveys and others 2003; Slot and Kitajima 2015; Carter and others 2020) but is represented by only a few studies with conflicting results on thermal acclimation potential for roots. In temperate hardwood forest warming experiments, ecosystem fine-root respiration has

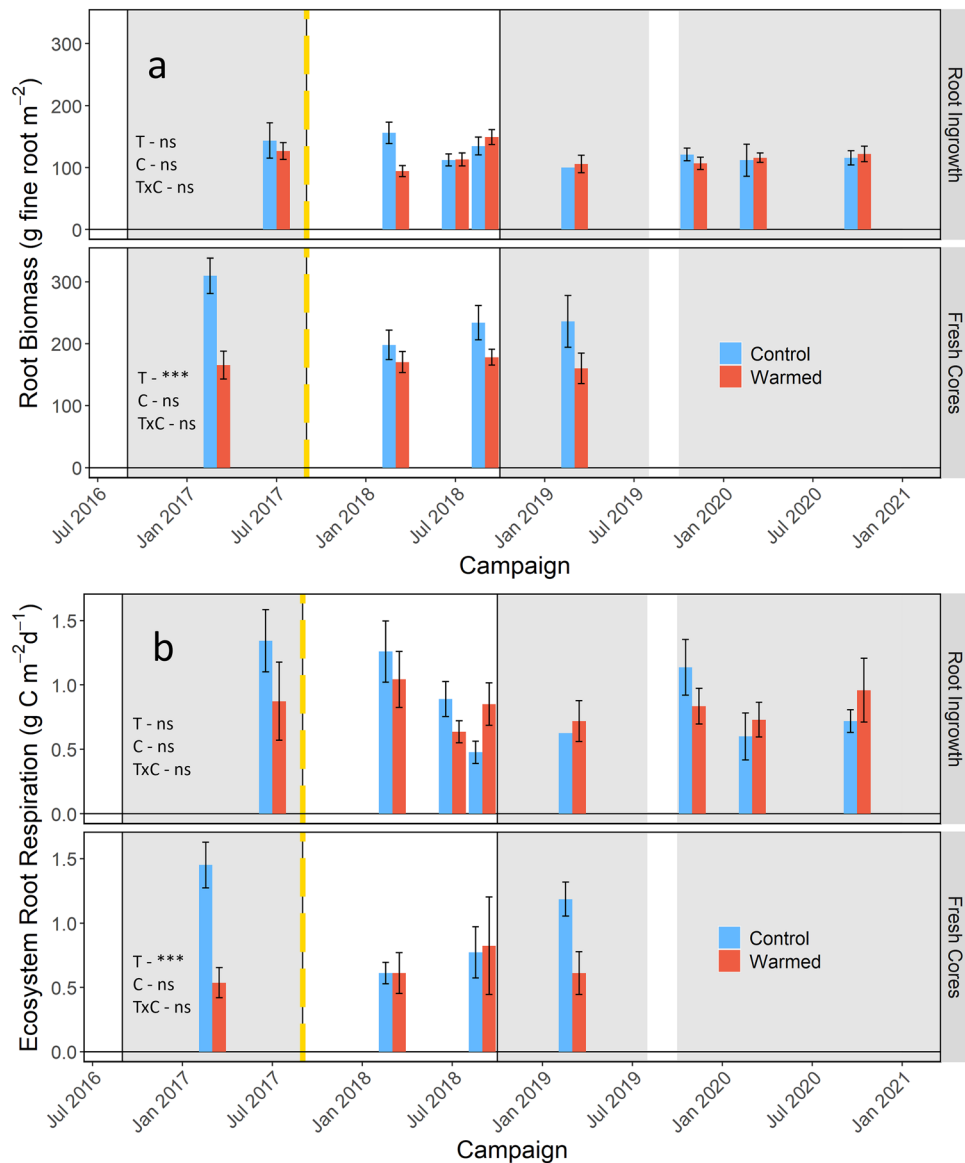


Figure 3. Root biomass per unit ground area in the upper 10 cm of soil (a) and estimated fine ecosystem root respiration at 25 °C per unit ground area for control and warmed plots during each sampling campaign (b). Root ingrowth campaigns are in the top panel and fresh core campaigns are in the bottom panel for each plot. Shaded blocks show where warming was turned on, and white blocks show where warming was not turned on. The legend in the bottom left shows where there is statistical significance for treatment (T), campaign (C), and treatment x campaign interaction (Tx) in an ANCOVA.

been observed to acclimate to warming through down-regulation of root biomass (Melillo and others 2011) and through down-regulation of root specific respiration at a standard measurement temperature of 18 °C (Jarvi and Burton 2013). Loveys and others (2003) did not observe root respiratory acclimation for greenhouse-grown temperate herbaceous plants, though they did see foliar thermal respiratory acclimation; while Atkinson and others (2007) found no change in root Q_{10} for greenhouse-grown temperate herba-

ceous plants. Thermal root respiratory acclimation was observed in a greenhouse study of sub-tropical citrus plants (Bryla and others 1997) and in one of four tropical species in a greenhouse study (Noh and others 2020). There was no evidence of thermal acclimation of root respiration in an in situ soil warming experiment in a tropical ecosystem in Panama (Nottingham and others 2020).

Prior to the 2017 hurricanes, warmed plots maintained much lower root biomass for fresh cores, showing only half as much root biomass as

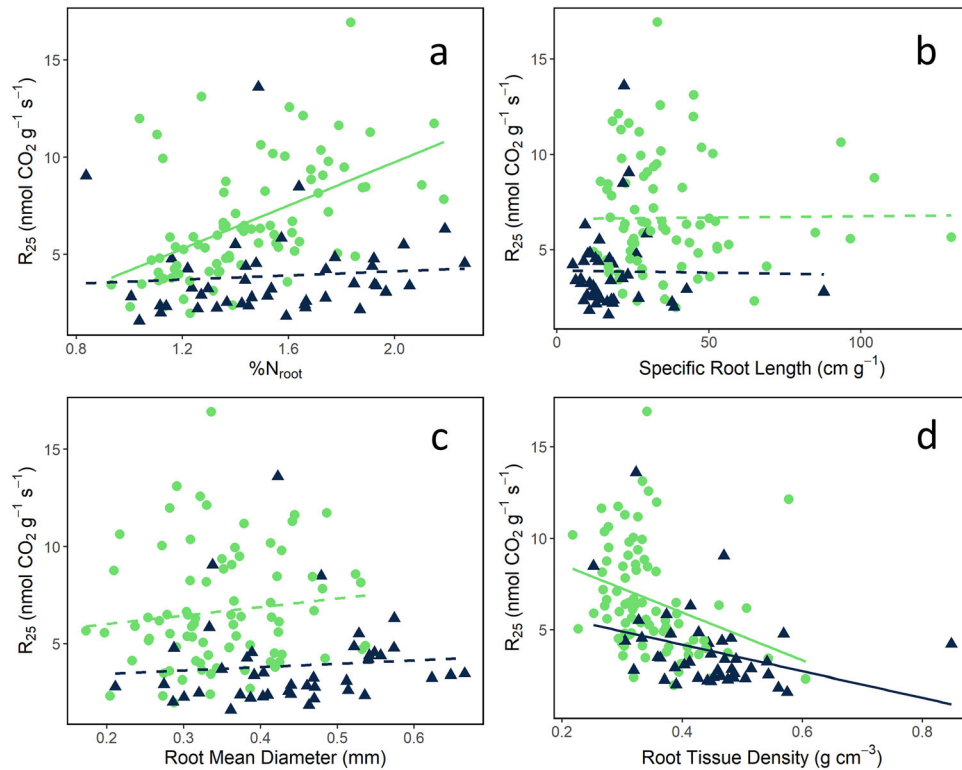


Figure 4. RSR_{25} relationships with root nitrogen content (**a**), specific root length (**b**), root mean diameter (**c**) and root tissue density (**d**). Root ingrowth cores are denoted by green circles and fresh cores are denoted by blue triangles. Solid lines indicate a significant correlation and dashed lines are not significant. RSR_{25} increased with higher root nitrogen content and decreased with higher root tissue density. RSR_{25} was not affected by root length or diameter.

the unwarmed controls (Figure 3a). This lower root biomass translated into much lower ecosystem root respiration rates (that is, per unit ground area; Figure 3b). This warming effect on root biomass and thus root ecosystem respiration was not seen in the root ingrowth cores, suggesting it was not warming's effect on root growth capacity that caused the response. The soil and roots within the fresh cores had been warmed for a much longer period of time than ingrowth core roots and also had nearly double the root biomass compared to the ingrowth cores. As such, we were able to use these two methods to ask rather different questions, with trade-offs for each. The ingrowth cores enabled us to assess more immediate mechanistic effects of warming and disturbance on the physiology of the youngest roots and new root growth. Fresh core data, on the other hand, provided a more time-integrated assessment of both warming and hurricane disturbance on the physiology and root mortality, and was a better indication of change in overall root biomass. There was likely not enough time to accrue a sufficient amount of root biomass in the root ingrowth cores to lead to a significant difference in root biomass between

treatments. In addition, all roots in root ingrowth cores were new growth, while fresh cores had a mixture of fine roots at different life stages. As such, greater rates of mortality may have been captured in warmed fresh cores where the soil had been warmed since the experiment began, while the ingrowth cores may not have had enough time to accumulate detectable differences in mortality. Ultimately, we believe the fresh core root biomass data are the most relevant for scaling the root respiration measurements to the ecosystem scale. The fresh core method was cumulatively too destructive within our small plots, however, so we incorporated and then transitioned to ingrowth cores after the first four fresh core campaigns. We expected warming to decrease ecosystem root respiration rates compared to control plots due to lower fine root biomass under warming (H2), and this hypothesis was partially supported by our data for pre-hurricane fresh cores. However, H2 was not supported post-hurricane because ecosystem root respiration was not affected by previous warming for root ingrowth or fresh cores when warming was not active, suggesting there was no legacy effect from warming, or that the treatment effect on root

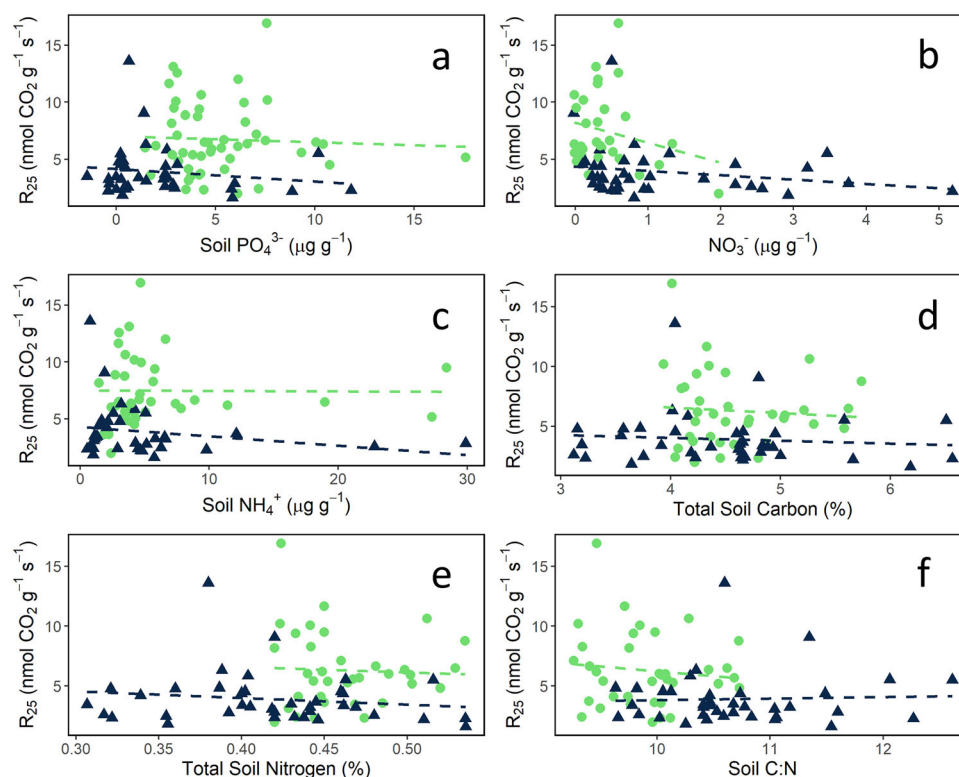
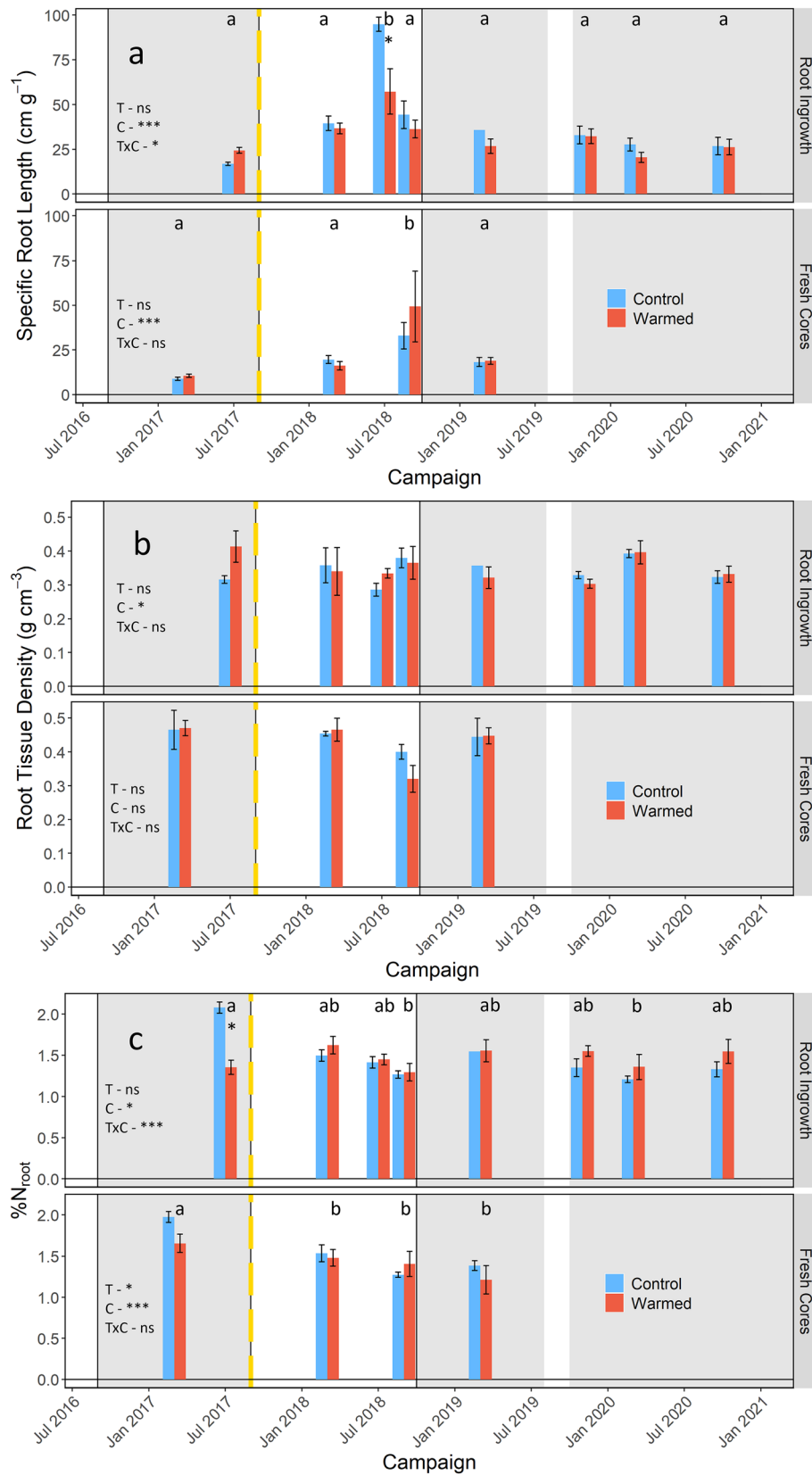


Figure 5. RSR_{25} relationships with soil phosphate (a), soil nitrate (b), soil ammonium (c), total soil carbon (d) total soil nitrogen (e) and soil C:N (f). Green circles are root ingrowth cores and blue triangles are fresh cores. Solid lines indicate a significant correlation and dashed lines are not significant. There were no significant relationships between RSR_{25} and soil nutrients.

biomass was not strong enough to be detected in our ecosystem root respiration response. While there was no difference in ecosystem root respiration for post-hurricane fresh cores when warming was active, there appears to be an emerging trend where control plots had a higher ecosystem root respiration rate. As succession proceeds, we predict to see this trend towards the values we observed for pre-hurricane warmed cores. While not statistically different, estimated means of ecosystem root respiration from fresh cores containing established roots were about 50% lower in the warmed plots than ambient temperature plots after the hurricanes when warming was turned back on because the warming treatment caused root biomass to decrease, but RSR_{25} had higher values and more variation for both control and warmed plots.

One potential bias in our data is that the magnitude of soil warming was lower at the site after the hurricanes than before due to higher vegetation density blocking the amount of IR radiation hitting the soil surface (Figure 1). While it is unlikely this had an effect on RSR_{25} and Q_{10} , because there were no warming effects on those parameters, it could have had a potential effect on overall

root biomass. The fact that we observed lower root biomass in warmed plots under both conditions indicates that the aboveground warming effect on plant tissues could be affecting belowground biomass. We suspect that the reason for this could be a biomass allocation with whole-plant controls rather than a change in root morphology to acclimate to warmer soil conditions. The belowground biomass allocation could be a product of biomass partitioning, or lower overall plant biomass, though these data were beyond the scope of our study. The change in plant community structure could also have differential effects on root biomass, but because we see the pattern of reduced root biomass reappear in the warmed plots, we think this could be an overall pattern for warmed species at our study site, independent of whether they are woody or herbaceous. Additionally, many of the roots collected in the cores may not be from plants exposed to the warming treatment, as many plants can have far-extending roots and our plots were only 4 m in diameter. Despite possibly being from outside of the plots, the majority of roots are likely from plants within the plots and exposed to the experimental warming treatment.



◀Figure 6. SRL (a), RTD (b), and N_{root} (c) for control and heated plots during each sampling campaign. Root ingrowth campaigns are in the top panel and fresh core campaigns are in the bottom panel for each plot. Shaded blocks show where warming was turned on and white blocks show where warming was not turned on. Hurricanes occurred at dashed yellow lines. The legend in the bottom left shows where there is statistical significance for treatment (T), campaign (C), and treatment x campaign interaction (TxC) in an ANCOVA. Characters indicate statistical significance between campaigns.

Overall, we found that ecosystem root respiration was lower in experimentally warmed plots, which is contrary to results from another in situ tropical warming experiment that did not see a difference in root respiration contributions to total soil respiration for warmed plots (Nottingham and others 2020). Using minirhizotron techniques at the TRACE study site, Yaffar and others (2021) found root production to decrease with warming post hurricanes, while root mortality showed no effect of experimental warming. This is in line with our fresh core root biomass data. The difference between our observed reduction in ecosystem root respiration and lack of difference observed by Nottingham and others (2020) was likely attributed to our direct measurement of root respiration and biomass, while the Nottingham and others (2020) study used indirect measurements of root respiration contributions to soil respiration via the use of root exclusion methods. If the root biomass changes in the Nottingham and others (2020) study are consistent with our observations, it is likely that the heterotrophic contributions to overall soil respiration were higher than observed in our study.

Higher heterotrophic respiration could be indicative of higher nutrient turnover by microbial processes that could be leveraged by plants producing fewer roots that can uptake more nutrients with less biomass. Microbial biomass for C and N is higher in warmed plots when warming is active, but there is no effect on microbial C and N after the hurricanes when warming was not active (Reed and others 2020).

If this is not an acclimation response, but rather a stress response, there could be indirect, detrimental effects on other plant processes like photosynthesis, water uptake, and nutrient acquisition. The TRACE warming experiment includes understory vegetation warming which can indirectly influence belowground biomass allocation and belowground CO_2 efflux. A limitation on photosynthetic uptake due to warming, which occurred for our understory shrubs (Carter and others 2020), may result in belowground root respiratory substrate limitation because of the linkages between above and belowground fluxes in tropical systems (Gutiérrez del Arroyo and Wood 2020, 2021). However, it was probably more likely that our patterns were driven by a limitation in root growth rather than respiratory substrate limitation, as we found no treatment effects in root specific respiration. We did, however, find a down-regulation of ecosystem root respiration which was largely driven by root biomass. Decreased fine root biomass could also limit water uptake which would decrease chances of survival during periods of soil water deficit. In addition, lower root biomass could decrease nutrient uptake, limiting the potential for aboveground plant structures to assimilate CO_2 .

Experimentally warmed temperate species have been found to allocate more carbon to belowground biomass than ambient temperature plants, and the effect sizes of increased fine root biomass in

Table 3. ANOVA Table for Fresh and Root Ingrowth Cores with Treatment, Campaign, and Their Interaction as Independent Variables

Core type	Factor	SRL (cm g^{-1})		RTD (g cm^{-3})		N_{root} (%)	
		df	P	df	P	df	P
Root ingrowth	Treatment	1	0.06	1	0.80	1	0.48
	Campaign	7	< 0.001	7	0.046	7	0.004
	Treatment:campaign	7	0.047	7	0.52	7	< 0.001
Fresh cores	Treatment	1	0.35	1	0.83	1	0.044
	Campaign	3	< 0.001	3	0.17	3	< 0.001
	Treatment:campaign	3	0.27	3	0.81	3	0.29

Statistically significant p values with $\alpha < 0.05$ are denoted with bold text.

warmed plants decrease with decreasing latitude, meaning warming affects root biomass production less the closer you get to tropics (Wang and others 2021). Experimental warming in temperate ecosystems can make temperatures closer to the photosynthetic temperature optimum, thereby increasing potential carbon fixation. In contrast, tropical plants are already at or near their photosynthetic temperature optima (Doughty and Goulden 2008; Mau and others 2018). This is important for contextualizing our root results, which show warming-induced decreases in biomass are contrary to the trend for non-tropical plants. Taken together, these temperate and tropical patterns suggest belowground carbon allocation may be mediated by total photosynthate production even in a warming world.

Hurricane Disturbance Response

Increased root specific respiration for root ingrowth cores immediately after hurricanes followed by a decrease several months later is likely caused by a quickly changing plant community composition after the hurricanes. The root ingrowth cores contained only new root growth, so they were likely dominated by the most recently grown plants. Our field site was about 70% bare ground, 20% herbaceous cover, and 10% woody cover before the hurricanes and shifted to 6% bare ground, 70% herbaceous cover, and 14% woody cover in September 2018, about a year after the hurricanes (Kennard and others 2020). Furthermore, plant community composition shifts causing respiration shifts is supported by changes in other root dimensional traits like root tissue density and specific root length because herbaceous plants are faster living and are likely associated with more acquisitive root traits that typically have higher root specific respiration.

Independent of warming or hurricane effects, RSR_{25} was about 1.7 times higher in root ingrowth cores than fresh cores (Figure 2a), suggesting that new root growth had higher metabolic demand than established roots had for maintenance and nutrient acquisition. Additionally, root ingrowth core RSR_{25} was more variable after the hurricanes, possibly due to species-specific differences in RSR_{25} and the dynamic changes in plant communities following disturbances. During the September 2018 campaign, low RSR_{25} values could be due to the plots being dominated by grasses while all other campaigns had lower grass density (Kennard and others 2020). In a study of species across biomes, including tropical species, eudicots had higher res-

piration rates than graminoids (Roumet and others 2016), which were much more abundant in the plots in the year following the hurricanes than they were before. In a study on root growth during primary succession in a post-mining site, plots in earlier successional stages had higher herbaceous root biomass and later successional plots had higher woody root biomass, suggesting that taxonomic class was important for describing root biomass in the soils at different successional stages (Kaneda and others 2022). Root ingrowth cores had higher variability following hurricanes, while fresh cores remained constant following hurricanes indicating that newly developed fine root RSR_{25} was more variable than established fine root RSR_{25} . Higher RSR_{25} variability in new fine roots, but not established roots, could indicate shifts in community composition. Though both root ingrowth and fresh cores were subjected to the same successional changes, root ingrowth cores were composed of strictly new growth, while fresh cores represented a mix of established roots and new roots. Additionally, root ingrowth cores contained the same homogenized soil that contained similar microbial communities and aggregates were broken up with no large rocks or other obstructions while fresh cores were intact undisturbed soils that had been “incubating” in place for years.

Higher root specific respiration in root ingrowth cores than fresh cores suggest root ingrowth cores have higher respiratory demand associated with new root growth or nutrient uptake while fresh cores are more associated with maintenance respiration. Post-hurricane variation of root specific respiration for root ingrowth cores but not fresh cores suggest the variation in root specific respiration is mainly influenced by new growth, and maintenance respiration is relatively unchanged. Our data suggest the “resilience debt” (that is, higher disturbance frequency leading to ecosystem dysfunction) for roots is more strongly affected by warming than hurricanes because the biomass in the fresh cores from the control plots recovered to pre-hurricane levels, while the biomass in the warmed plots was unchanged after the hurricanes, and was consistently lower than biomass in the control plots.

Relationships Between Root Respiration, Root Traits, and Soil Nutrients

We expected a nutrient pulse after the hurricanes to cause roots to switch to more acquisitive strategies for nutrient uptake (H3). Root specific respiration, however, was apparently not affected by

extractable soil NO_3^- , NH_4^+ , or PO_4^{3-} . Root biomass did not increase after the hurricanes, but our temporal resolution may not have been fine enough to capture the sharp peak in root biomass immediately after hurricane disturbance observed in other studies (Silver and Vogt 1993; Yaffar and others 2021). H3 was partially supported in that RSR_{25} showed a positive relationship with N_{root} , and a negative relationship with root tissue density, which are both indicators that the higher respiration roots were exhibiting more acquisitive root traits and lower respiration roots were more conservative (Roumet and others 2016). While some of the higher respiration from root ingrowth cores could be a product of a more acquisitive strategy, much of it is likely from new root growth, which also has high metabolic demand and is associated with higher N concentration for growth. Specific root length increased following the hurricanes, while root specific respiration remained constant, indicating root morphology changed to make more efficient use of energy by increasing root length, while still using the same amount of energy per unit mass.

CONCLUSIONS

Overall, we did not observe acclimation of tropical forest root respiration to experimental warming through direct controls over respiratory mechanisms, but we did see ecosystem root respiratory acclimation through decreased fine-root biomass in the upper 10 cm of soil. Decreased root biomass was likely driven by experimental warming, though it is unclear if the warming effect was caused by above or belowground effects of warming. While the hurricanes increased the variability we observed in many of our responses, most variables appeared to return to pre-hurricane levels within two years. Hurricanes make it challenging to study the effects of warming alone, but offer valuable insight into root responses to disturbance. Lower ecosystem root respiration in a warmer world means that tropical roots may have a smaller contribution to atmospheric CO_2 than they do now, but decreased root biomass could have downstream implications for aboveground processes caused by potential changes in nutrient and water uptake. We speculate these changes could result in decreased CO_2 assimilation through photosynthesis, which could be confirmed through modeling net ecosystem productivity.

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DATA AVAILABILITY

Data are available through ESS-DIVE at <https://data.ess-dive.lbl.gov/view/doi:10.15485/2007467>.

Declarations

Conflict of interest The authors do not have any conflicts of interest.

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