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Warming exerts greater impacts on subsoil than topsoil CO_2 efflux in a subtropical forest

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ABSTRACT

How warming affects the magnitude of CO_2 fluxes within the soil profile remains an important question, with implications for modeling the response of ecosystem carbon balance to changing climate. Information on belowground responses to warming is especially limited for the tropics and subtropics because the majority of manipulative studies have been conducted in temperate and boreal regions. We examined how artificial warming affected CO_2 gas production and exchange across soil profiles in a replicated mesocosms experiment relying on heavily weathered subtropical soils and planted with Chinese fir (*Cunninghamia lanceolata*). Half of 2 × 2 m mesocosms (5 replications) was heated with cables buried at a 10 cm depth, which increased temperature in the whole soil profile by 4.5, 3.6 and 2.5 °C at 15, 30 and 60 cm soil depths, respectively. Using a combination of chamber-based and concentration gradient method (CGM) approaches, we found that warming increased soil CO_2 efflux across the whole profile by 40%. Changes were unevenly distributed across soil depth: mean CO_2 production rate decreased from 0.74 to 0.67 μmol CO_2 m^{-2} s^{-1} in topsoils (0–15 cm depth) whereas it increased from 0.26 to 0.73 μmol CO_2 m^{-2} s^{-1} in subsoils (15–60 cm depth). Warming reduced moisture more strongly in subsurface than surface soils and increased subsoil soluble N concentrations as well as fine root turnover, in line with previous temperate and boreal warming studies. This consistency indicates that overall responses of subtropical forests to warming may be similar to forests in higher latitudes.

1. Introduction

Small changes in the global balance of C inputs to and losses from soil can exert a significant influence on atmospheric [CO_2]. However, there is significant uncertainty about temperature controls on the loss term in the soil C storage equation (Giardina et al., 2014; Bradford et al., 2016; Jackson et al., 2017), in part because our understanding of soil C formation and subsequent decomposition is poor. This uncertainty is particularly strong for tropical and subtropical forests (Piao et al., 2013; Cavaleri et al., 2015; van Gestel et al., 2018). Efforts directed at understanding the response of C process rates to change, particularly in deeper soil horizons, is critical to reducing this uncertainty (Rumpel and Kögel-Knabner, 2011). Despite occurring at relatively low concentrations, total C stored below 20 cm accounts for more than 50% of the world's soil organic carbon (SOC) (Jobbágy and Jackson, 2000; Jackson et al., 2017). Therefore, even small changes in belowground process rates could play a significant role in shaping the CO_2 source or sink strength of the atmosphere.

The potential mechanisms for subsoil C stability can be summarized as follows: C input into subsoils is derived by plant roots or/and the microbial decomposition products of plant litters (Kuzyakov and Blagodatskaya, 2015; Giardina et al., 2014), both of which can be chemically more resistant to decomposition than fresh litter on the soil surface (Nierop, 1998; Lorenz and Lal, 2005; Rumpel and Kögel-Knabner, 2011). In addition, the transport of enzymes, substrates, water, oxygen and microorganisms is limited in deeper parts of the soil profile (Rumpel and Kögel-Knabner, 2011), which can contribute to a spatial separation of microbes and C inputs, which slows the turnover of

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deep soil C (Lützow et al., 2006; Holden and Fierer, 2005). Similarly, Lützow et al. (2006) and Schmidt et al. (2011) argue that biotic and abiotic environmental factors are more important than C quality in determining C stability in deep soil.

Dozens of field experiments and laboratory incubation studies in temperate and boreal zones have documented positive soil organic matter (SOM) decomposition responses to warming, as well as increases in the concentrations of dissolved organic carbon (DOC) and NO_3^- availability caused by experimental warming, which can accelerate C and N leaching to deeper soil (Lu et al., 2013; Bai et al., 2013; Crowther et al., 2016). Warming-induced declines in soil moisture can increase gas diffusivity, enhance root growth but also increase root mortality in the soil profile (Lu et al., 2013; Yang et al., 2013). The extent to which these observed responses to warming also characterize responses in the tropics is unknown.

South China has a monsoonal climate, and the climax vegetation of this region is subtropical evergreen broadleaved forest developed on highly weathered soils (Huang et al., 2013). Due to increasing demand for timber and other forest products over the past several decades, most native broadleaved forests have been harvested, and were subsequently converted to plantations of more productive tree species, especially Chinese fir (*Cunninghamia lanceolata*) (Yang et al., 2009), which now covers over 9 million ha and accounts for 30% of all plantations in China (Lei, 2005). To understand how global warming will affect ecosystem C balance in the tropics, we established a soil warming mesocosm experiment in Fujian Province, China (Liu et al., 2017). We planted this experiment with Chinese fir because of its widespread use across the region as a premier plantation species. We selected a heavily weathered soil typical of subtropical plantation forests in south China, and broadly representative of tropical forest soils. Building on previous work at this site (Liu et al., 2017), we used these replicated mesocosms to examine vertical CO_2 fluxes from subsurface and surface soils as well as efflux at the soil surface. To understand the mechanisms involved in the CO_2 fluxes across soil profiles, we examined *in-situ* soil moisture, temperature, nutrients, DOC and fine roots (Fierer et al., 2003).

We hypothesized that soil warming increases: (1) CO_2 production rates, with proportionally higher contribution to CO_2 production in subsoil due to enhanced microbial activities and root growth (Fontaine et al., 2007); (2) fine root turnover rate and distribution in subsoil where warming reduces water availability (Hendrick and Pregitzer, 1996; Hutchings and John, 2003); and (3) DOC concentrations and N availability in subsoil because of enhanced mortality rates for fine roots, and warming-induced N leaching (Lu et al., 2013; Yang et al., 2013).

2. Materials and methods

2.1. Research area description

This study was conducted in the Chenda Observation Study Site of Sanming Forest Ecosystem and Global Change Research Station (26°19′3″ N, 117°36′22″ E, 300 m a.s.l) in Fujian Province with 66% of forest cover. Native forest vegetation in this region is dominated by evergreen broadleaf species, the majority of which are in the Fagaceae family. The Sanming Research Station is characterized by a typical maritime subtropical monsoon climate with a mean annual temperature (MAT) of 19.1 °C. Temperature extremes occur in January (mean monthly temperature of 9.7 °C) and in July (mean monthly temperature of 28.2 °C). Mean relative humidity, mean annual precipitation (MAP) and mean annual potential evapotranspiration are 81%, 1750 mm and 1585 mm, respectively. Precipitation from March to August accounts for > 70% of the total annual precipitation. Soils at the site are classified as red soils according to China's soil classification categories equivalent to Oxisols in USDA soil taxonomy (State Soil Survey Service of China, 1998; Soil Survey Staff of USDA, 2014).

2.2. Experimental design

Details of the experimental design have been previously reported (Liu et al., 2017, but briefly we established a mesocosm warming experiment in August 2013. Five control and five warming 2 m × 2 m plots were established, with PVC boards (0.8 cm thick) inserted to a depth of 70 cm to separate plots from adjacent plots and surrounding soil. Subsequently, heating cables (TXLP/1, Nexans, Norway) contained a resistance wire with an output of 17 W m^{-1} at 230 V were installed at a soil depth of 10 cm. The distance between cables was 20 cm. Temperature increase of 5.0 °C was targeted based on the RCP 8.5 scenario's prediction and the information that majority of studies in the temperate and boreal forests used 3–7 °C increase as warming treatment (Bronson et al., 2008; Melillo et al., 2002). Soil temperature sensors (T109 from Campbell Scientific Inc., Logan, UT, USA) were placed between two cable lines (6 m long per square meter) at a soil depth of 10 cm in each plot. Three temperature sensors were installed in each warming plot and two in each control plot. Soil moisture for 0–10 cm soil layer was measured with 2 ECH2O-5 soil moisture probes (Decagon, Pullman, Washington, USA). Soil temperature and moisture were recorded at 30-minute intervals.

In November 2013, four one-year-old Chinese-fir seedlings were planted in each plot between the cables. The 40 Chinese-fir seedlings were carefully selected from more than 1000 seedlings to minimize variability in height, basal diameter, and size of the root system. Based on previous work with this species, the Chinese-fir seedlings grew normally after planting. Warming started on March 1, 2014 and data were not collected until May of 2014.

2.3. Soil CO_2 gas concentration measurements

Soil gas from different depths was sampled using gas wells (Breecker et al., 2012; Maier and Schack-Kirchner, 2014; Oerter and Amundson, 2016). Three sampling tubes (DIK-5212, Japan) were installed vertically at the depths of 15, 30 and 60 cm in each plot in March 2014. Once installed, each sampling tube was sealed to gases other than those diffusing in from the soil layer being sampled. A medical syringe was connected to the three-way cock valve when sampling the soil gas. The syringe piston was retracted slowly to reduce soil disturbance, and to ensure gas sample integrity (Hashimoto et al., 2007; Maier and Schack-Kirchner, 2014). Soil gas was sampled biweekly using a syringe from May 2014 to May 2015. The collected soil gas was injected into a gas bag (Delin, China) and immediately sent to the laboratory to determine CO_2 concentration with gas chromatography (Shimadzu gas chromatograph, Japan).

In each plot, three multifunction sensors (5TE, Decagon Devices Inc., USA) were installed next to the gas sampling tubes and connected with a self-contained digital data logger (EM50, Decagon Devices Inc., USA) to measure soil temperature and moisture at depths of 0–20, 20–40 and 40–60 cm at an interval of 30 min.

2.4. Soil CO_2 production calculation and validation

In this study, the flux of CO_2 diffused through each layer was calculated from D_s and the discrete difference in the CO_2 concentration across each layer according to Fick's first law of diffusion:

$$F_S = -D_s \frac{\Delta C(z)}{\Delta z} \tag{1}$$

Where F_s is the CO_2 efflux (μmol m^{-2} s^{-1}), D_s is the CO_2 diffusion coefficient in the soil (m^2 s^{-1}), C is the CO_2 concentration (μmol m^{-3}) at soil depth of z (m), and $\frac{\Delta C(z)}{\Delta z}$ is the vertical soil CO_2 gradient. D_s was estimated as

$$D_s = \xi D_a \tag{2}$$

Where ξ is the gas tortuosity factor, and D_a is the CO_2 diffusion coefficient in the free air (Jury and Horton, 2004), which is adjusted by soil temperature at corresponding soil depth and air pressure. The effect of temperature and pressure on D_a was accounted for with the equation,

$$D_a = D_{a0}\left(\frac{T}{293.15}\right)^{1.75}\left(\frac{P}{101.3}\right) \quad (3)$$

Where T is the temperature (K), P is the air pressure (kPa), D_{a0} is a reference value of D_a at 20 °C (293.15 K) and 101.3 kPa, and D_a is given as 14.7 mm^2 s^{-1} (i.e. T = 20 °C or 293.15 K, P = 1.013 × 10^5 Pa, $D_a = 1.47 \times 10^{-5}$ m^2 s^{-1}) (Jones, 1992).

D_s is a crucial parameter for the flux calculation using the CGM. Thus, we used five empirical models for calculating ξ (Penman, 1940; Millington, 1959; Millington and Quirk, 1961; Moldrup et al., 1997, 2000) in order to compare the modeling results with the values measured with Licor-8100. We chose the Moldrup-2000 model (Moldrup et al., 2000) because it produced the best agreement with chamber based estimates of soil surface CO_2 efflux, which is estimates as below:

$$\xi = \frac{(\phi-\theta)^{2.5}}{\phi} \quad (4)$$

Where θ is the volumetric water content (cm^3 cm^{-3}), ϕ is the porosity (Moldrup et al., 1997, 2000). Porosity was estimated as= $\frac{\rho_b}{\rho_m}$, where ρ_b is the bulk density (g cm^{-3}), and ρ_m is the particle density, which was 2.63 g cm^{-3} for our mineral soil.

The calculated fluxes were assigned to the center of each layer while flux for the topsoil layer was assigned to the soil surface (See Maier and Schack-Kirchner, 2014). The CO_2 production in each soil depth (P_{CO_2}) was calculated as the change in the flux (F_{CO_2}) from the center of one layer $(F_{CO_2})_1$to the center of the next layer $(F_{CO_2})_2$ (Maier and Schack-Kirchner, 2014). We ignored any possible changes in soil CO_2 storage, because the change in amount of CO_2 stored in a soil layer is negligible compared with F_{CO_2} (Risk et al., 2002a, b; Hashimoto et al., 2007). In summary, the P_{CO_2} in a soil layer was calculated by the difference in cumulative CO_2 emitted at the soil layer boundaries (Risk et al., 2002a, b):

$$P_{CO_2} = (F_{CO_2})_1-(F_{CO_2})_2 \quad (5)$$

The CO_2 production in the deepest layer was defined by the flux at the bottom (Hashimoto et al., 2007). To validate biweekly CGM results from May 30, 2014 to May 15, 2015, and to compare various models, CO_2 efflux from the soil surface was also manually measured using a closed chamber technique.

2.5. Soil sampling and analysis

On April 30, 2015, six soil cores (60 cm) were randomly collected from each plot for physical and chemical analyses. All sampling was completed within 2 h using a 2-cm soil coring device (New landmark soil equipment Co., Ltd, China). A soil core of 5 cm in diameter was used for sampling soil bulk density. Soil samples were placed in an icebox and transferred to the laboratory for analysis. Each soil core was separated into three layers: 0–20, 20–40 and 40–60 cm. Soil samples were passed through a 2-mm-mesh sieve to remove roots, organic debris and stones. The sieved soils were then stored in a refrigerator at temperature of 4℃ for a maximum of one week before analysis. Each processed sample was divided into two sub-subsamples, one for analysis of DOC, DON, nitrate (NO_3^-) and ammonium (NH_4^+) and the other for soil C and N determination under high-temperature oxidation using CN analyzer (Elementar Vario MAX, Germany). Soil texture was determined using laser granulometer (MasterSizer2000, UK). Soil pH was determined using pH meter with soil to water ratio of 1:2.5 in weight, and DOC and DON were determined using SHIMADZU TOC-VCPH/CPN analyzer (Wan et al., 2015). Soil nitrate NO_3- and NH_4^+ analyses were conducted using Continuous Flow Analyzer (SKALAR San++, Holland).

2.6. Fine root growth and mortality

To monitor fine root growth and mortality, in August of 2013 we used minirhizotrons, two of which were installed in each plot by inserting into soil at an inclination angle of 45°. Data collection with a Minirhizotron Camera System (I-CAP version 4.01, Bartz Technology Coro, Carpinteria, USA) began in May 2014, 6 months after setting up the minirhizotrons. The digital image recorded at each sampling point had a size of 14 × 18 mm with ~40 frames taken for each tube. Root diameters, new root production, length of live roots, and root mortality were recorded accordingly.

2.7. Data analysis

The statistical analyses were performed using SPSS 20 (SPSS Inc., Chicago, IL, USA) for windows. Data normality was assessed using the Kolmogorov–Smirnov test, while homogeneity of variance was examined using Levene's test. When normality and homogeneity of variance assumptions were not satisfied, data were log transformed. Repeated-measures ANOVA was used to investigate the effects of warming on CO_2 concentration and production rates, as well as soil temperature and soil moisture at each soil depth (between May 2014 and May 2015). Independent-Samples *t*-test was used to determine the significance among treatments in the fine root production, fine root mortality, soil physical and chemical parameters, and soil CO_2-related variables at each soil depth. Polynomial regression models were applied to examine the relationship between soil CO_2 production and soil moisture. To assess which variables (include soil properties, fine root production, fine root mortality, soil temperature and soil moisture) were the most important drivers of the change in CO_2 production between control and warming treatment, a random forest analysis for regression (Breiman, 2001) was conducted using the *"randomForest"* package (Liaw and Wiener, 2002). Random forest is a nonparametric machine-learning algorithm (Breiman, 2001) that does not assume any data distribution and does not require any predictor selection (Cutler and Stevens, 2006; Cutler et al., 2007). The error rates of the random forest for the CO_2 production rate were decreasing when more trees were grown, and the error rates finally reached a stable level (1000 trees). Thus, we fitted a forest of 1000 multiple decision trees. The significance of the random forest model was tested with 9999 permutations of the CO_2 production rate in the *"rfUtilities"* package (Evans and Murphy, 2016). The significance of the relative importance for each the explanatory variable on each response variable was determined by assessing the decrease in prediction accuracy (Percentage of increase in mean square error), and a total of 9999 permutations of the CO_2 production rate were implemented by using the *"rfPermute"* package (Archer, 2013).

3. Results

3.1. Effects of warming on soil temperature and moisture

Increases in soil temperatures across this one year study were significant ($p < 0.001$), averaged 4.5 °C, 3.6 °C and 2.5 °C at depths of 0–20, 20–40 and 40–60 cm respectively, with maximum increases in summer (June and July) and minimum increases in winter (January and December) (Fig. 1a–c).

Soil warming significantly ($p < 0.001$) reduced soil moisture at all depths (Fig. 1d–f; Fig. 2b). Soil moisture in the warming treatment across this one year study averaged 18.2, 20.8 and 25.6% for 0–20, 20–40 and 40–60 cm, respectively. The corresponding averages for control plots were 23.5, 28.0 and 40.1%, respectively.

3.2. Soil CO_2 concentrations depending on soil depths

Soil CO_2 concentrations increased with depth for both control and

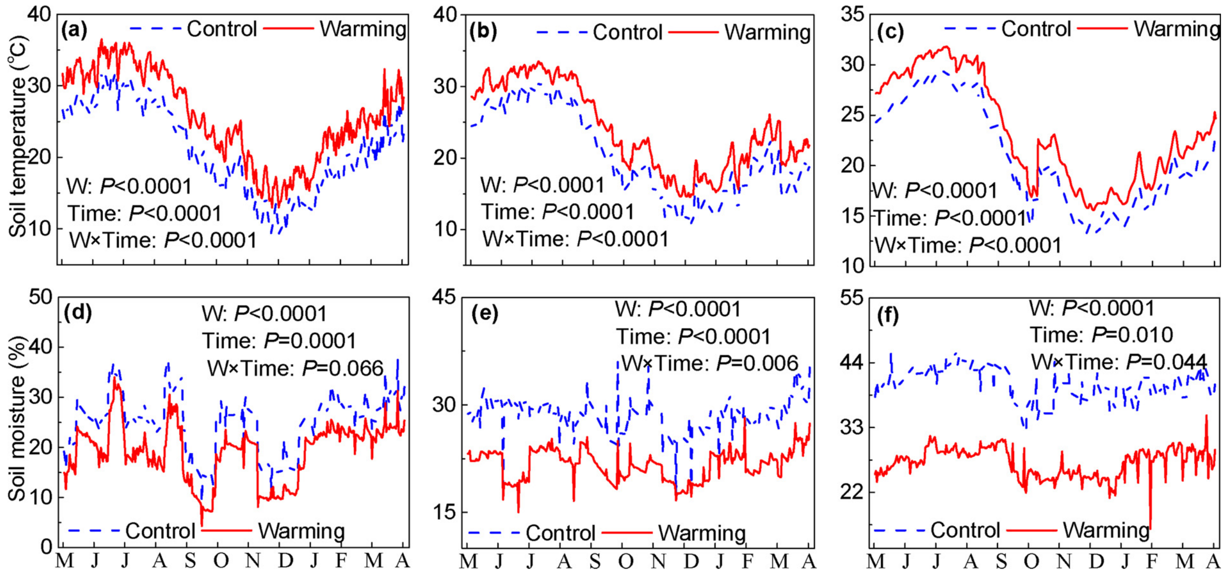

Fig. 1. The dynamics of soil temperature and soil moisture at the different soil depths during the period May 2014 – May 2015 for the warming treatment and the control (n = 5 samples, mean ± 1 SE). The upper left corner (a), (b), (c) indicated soil temperature at 0–20, 20–40 and 40–60 cm; (d), (e), (f) indicated soil moisture at 0–20, 20–40 and 40–60 cm. W: warming effect; Time: time effects. X-axis indicated month/year.

warming treatment. There was no difference between treatments for either mean annual CO_2 concentration or annual time course of CO_2 concentration at any soil depths (Fig. 3). Mean annual soil CO_2 concentrations (± 1 SE) for the control were 531 ± 34, 2984 ± 371, 4196 ± 509 and 9192 ± 1612 ppm at depths of 0, 15, 30, and 60 cm, respectively, being 529 ± 11, 2854 ± 120, 4399 ± 275 and 8292 ± 656 ppm for the corresponding soil layers in the warming treatment.

3.3. Soil CO_2 flux, production and depth contribution

There was a significant correlation between CO_2 fluxes derived from the diffusivity model (Moldrup et al., 2000) and those measured using the LI-8100 A closed chamber system, with linear correlation coefficients of 0.96 and 0.95 for the warming and control treatments, respectively (Fig. 4c). Soil warming increased CGM-based total soil CO_2 fluxes during the study period, with a mean across the study period of 1.4 ± 0.07 for the warming and 1.0 ± 0.05 μmol CO_2 m^{-2} s^{-1} for the control soil (Fig. 4b). The chamber-based approach to measuring soil CO_2 fluxes resulted in averages of 1.7 ± 0.06 and 1.4 ± 0.05 μmol CO_2 m^{-2} s^{-1} for warming and the control, respectively (Fig. 4a). The differences between CGM and chamber-based approaches may have arisen because flux calculations for the CGM approach relied on estimated soil physical parameters, for example the gas tortuosity factor, and relatively coarse measurements of bulk density, which together might not have been precisely representative of actual gradients across profiles. Further, while CGM derived CO_2 flux estimates agree closely to chamber measurements during stable weather conditions, they may deviate during and after rain for a short time (Jassal et al., 2005; Riveros-Iregui et al., 2008). In fact, our CGM based estimates of CO_2 efflux were about 20% lower than chamber-based estimates (Fig. 4). This discrepancy was possibly due to the linearization approach in CGM estimations while the actual CO_2 concentration was not linear, or resulted from diffusivity estimations rather than the CO_2 concentration and gradient measurements (Tang et al., 2003). Because of the strong overall agreement with chamber measurements, we suggest that observed patterns and changes caused by experimental warming are real.

A clear seasonal pattern in CGM based estimates of total CO_2 production rate was observed for both warming and control, with maxima in September and minima in February (Fig. 5). However, there were important differences between treatments: Soil warming increased CO_2 production ($p < 0.05$) in 15–30 and 30–60 cm depth soil layers of but reduced CO_2 production in the 0–15 cm layer. The CO_2 production in the 0–15, 15–30 and 30–60 cm depth soil layers were 0.62, 0.37 and 0.36 μmol CO_2 m^{-2} s^{-1} respectively in the warming treatment and

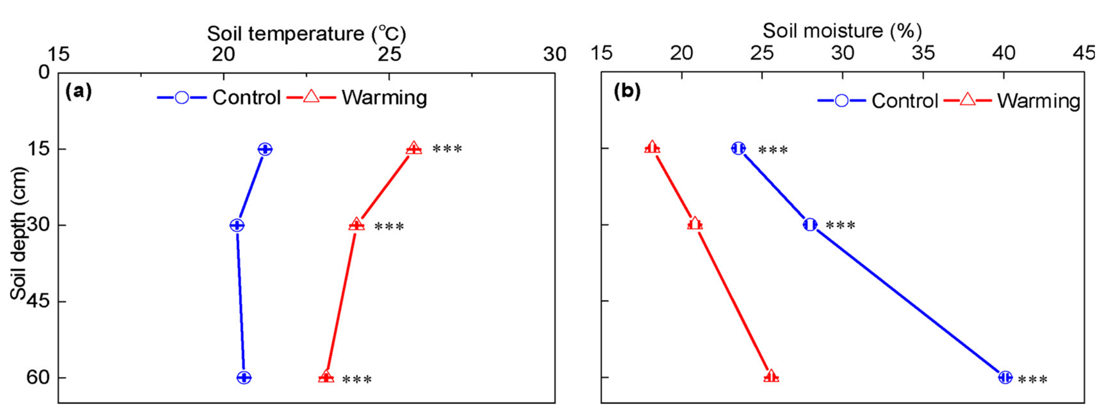

Fig. 2. The mean annual soil temperature (a), and the mean annual soil moisture (b) at 0–20, 20–40 and 40–60 cm in the warming treatment and the control. Error bars are standard errors (SE, n = 5). "***" indicate significant differences between control and warming treatment at $P < 0.001$.

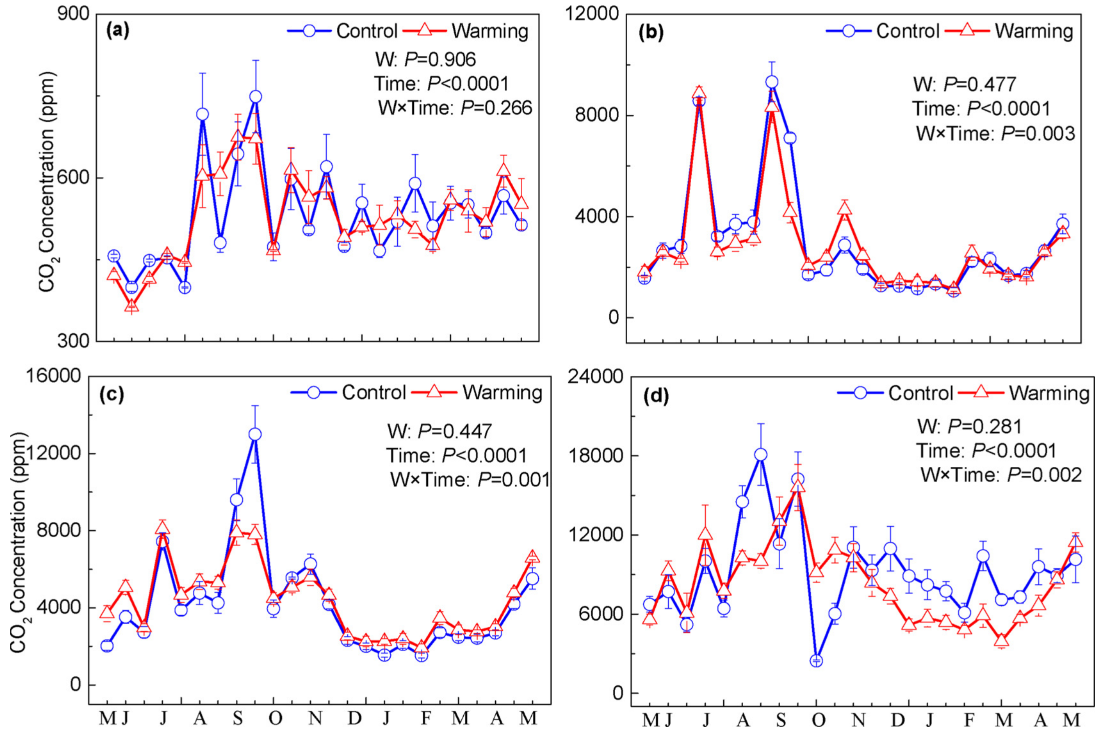

Fig. 3. The dynamics of soil CO_2 concentration at different soil depths during the period May 2014 – May 2015 for the warming treatment and the control (n = 5 samples, mean ± 1 SE). The upper left corner (a), (b), (c) and (d) indicated 0, 15, 30 and 60 cm. W: warming effect; Time: time effects.

0.73, 0.14 and 0.12 μmol CO_2 m^{-2} s^{-1} in the control.

Warming altered the distribution of CO_2 production across depths such that the contribution of each depth to total CO_2 production varied between treatments (Fig. 6c). The contribution of soil depth to total soil CO_2 production in 0–15 cm soil layer in the warming treatment was lower than the control (74 versus 46%, $P < 0.001$). The contribution of soil depth to total soil CO_2 production in the 15–30 and 30–60 cm soil layers in the warming treatment were higher than the control: both 27% in the 15–30 and 30–60 cm soil layers of the warming treatment, and 14 and 12% for the control, respectively.

3.4. Effects of warming on soil properties

Soil warming increased DON and NO_3^- concentrations in soil layers (Table 1, $p < 0.05$). There were no differences between the warming treatment and the control in total soil C, N, DOC, NH_4^+ and pH (Table 1). DON contents were 5.93 ± 2.2, 5.98 ± 3.3 and 5.25 ± 2.0 mg kg^{-1} in the soil layers of 0–20, 20–40 and 40–60 cm in the warming treatment, respectively and the corresponding values in the control were 2.04 ± 0.45, 0.8 ± 0.52 and 0.78 ± 0.69. Warming increased DOC by 191, 648 and 573% in the 0–20, 20–40 and 40–60 cm soil layers, respectively. Extracted NO_3^- were 7.89 ± 2.6, 7.51 ± 3.1 and 7.24 ± 2.5 mg kg^{-1} at the soil layers of 0–20, 20–40 and 40–60 cm in the warming treatment, respectively and 3.19 ± 0.52, 1.53 ± 0.39 and 1.6 ± 0.71 in the control, representing warming related increases of 250, 490 and 450% for 0–20, 20–40 and 40–60 cm depth soils, respectively.

Warming increased gas diffusivity across depths (Fig. 7). In the control, gas diffusivity was 1.93 ± 0.04, 1.24 ± 0.03 and 0.20 ± 0.005 mm^{-2} s^{-1} at 0–15, 15–30 and 30–60 cm soil depths, whereas in the warming treatment, gas diffusivity was 2.67 ± 0.05, 1.81 ± 0.03, 0.74 ± 0.01 mm^{-2} s^{-1} respectively, representing increases of 38.6, 46.2 and 275.8%.

3.5. Effects of warming on the production and mortality of fine root

Fine root production in 20–40 and 40–60 cm depth soils across the experiment averaged 15.6 ± 2.8 and 5.5 ± 0.7 m m^{-2} $month^{-1}$ in the control and 22.6 ± 3.3 and 15.4 ± 2.1 m m^{-2} $month^{-1}$ in the warming treatment, respectively (Fig. 8a). Mortality in control plots

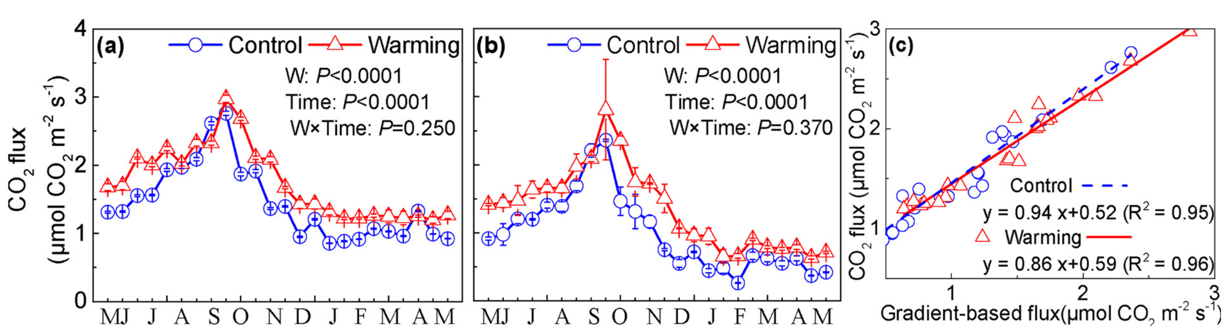

Fig. 4. The regression between soil CO_2 fluxes measured with LI-8100 and CO_2 fluxes derived from the diffusivity model by Moldrup et al. (2000). (a) denotes soil CO_2 flux by LI-8100, (b) denotes gradient-based flux, and (c) denotes the fitting between soil CO_2 flux by LI-8100 and the gradient-based flux. W: warming effect; Time: time effects. X-axis indicated month/year.

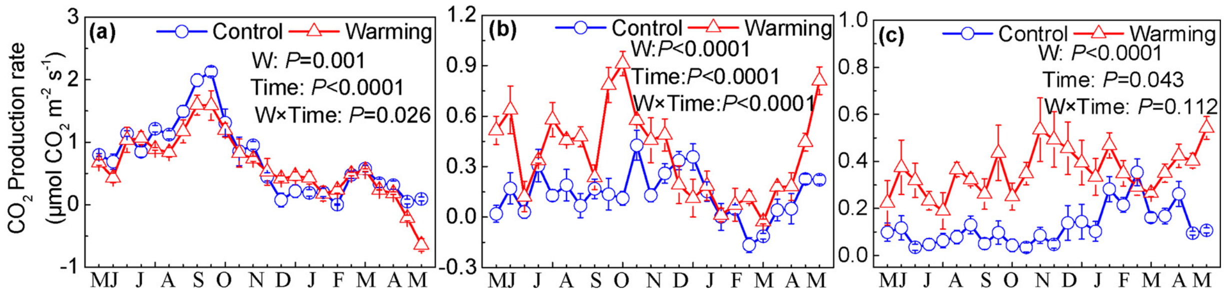

Fig. 5. The dynamics of soil CO_2 production rate at the different soil depths during the period May 2014 – May 2015 for the warming treatment and the control (n = 5 samples, mean ± 1 SE). The upper left corner (a), (b), and (c) denotes soil depth: 0–15, 15–30 and 30–60 cm. W: warming effect; Time: time effects. X-axis indicated month/year.

during the experiment averaged 6.0 ± 0.9 and 1.6 ± 0.2 m m^{-2} $month^{-1}$ for 20–40 and 40–60 cm, respectively but averaged 8.5 ± 0.2 and 4.4 ± 0.7 m m^{-2} $month^{-1}$ for the two depths in the warming treatment (Fig. 8b).

3.6. Relative importance of abiotic and biotic factors on soil CO_2 production

Temperature, moisture, the production of root, the mortality of root, DON and NO_3^- were the best predictors of variables in the CO_2 production at the layers of 15–30 and 30–60 cm (Table 2). While temperature, moisture, the production of root, DON, NO_3^-, NH_4^+ and DOC were the best predictors of variables in the CO_2 production at the layers of 0–15 cm.

4. Discussion

4.1. Warming effects on soil temperature and moisture

Nearly all manipulative warming experiments have focused on temperate and boreal ecosystems (Cavaleri et al., 2015; Hicks pries et al., 2017). We examined how warming affects belowground C process rates in a subtropical ecosystem including both surface and subsurface soils. A global synthesis by Carey et al. (2016) reported that experimental warming increased soil temperatures by 1.91 °C on average. While heating cables were buried to a 10 cm depth, as with a diversity of other warming studies, soils temperatures in our warmed plots were 4.5, 3.6 and 2.5 °C higher than controls at 15, 30 and 60 cm depths, respectively. The greater transfer of thermal energy deeper into soil profile compared with average responses encountered in temperate or boreal sites could reflect the combination of soil physical, chemical and climatic factors characterizing our study site. For example, mild winters in our sites may allow for enhanced warming of deeper soils. Further soil physical property differences could promote deeper movement of heat into soils. Soils at our site are clay developed from coarse granite, with a moderate sand content (Table 1), which when combined with high moisture content (Fig. 2), can contribute to high thermal conductivity. Differences in soil heating may also reflect methodological differences across reviewed sites. For example, experiments that warmed via electric cables documented the greatest average soil temperature increase (3.6 °C, n = 5), followed by infrared (2.3 °C, n = 11) and then passive (0.4 °C, n = 11) warming (Carey et al., 2016). While we suspect that mild winters and year round heating may allow for enhanced warming of deeper soils (most higher latitude experiments do not warm sites year round), more work is needed across a range of tropical sites to understand if our findings are generalizable to other tropical locations.

Manipulative warming often affects soil moisture (Carey et al., 2016). A meta-analysis by Xu et al. (2013) showed experimental warming decreased soil moisture across studies, with the largest reduction (11.7%) observed for forests. In our study, soil warming reduced soil moisture 22.8% in surface soils and 36.3% in subsurface soils. The stronger effect in the deeper soil may be due to increased root activity at depth, in addition to increased physical process of evaporation. In response to the moisture changes (Fig. 1), plants typically shift C allocation belowground to enhance soil moisture acquisition (Schenk and Jackson, 2002; Mokany et al., 2006). An expanding root system and greater carbon supply to mycorrhizae allows plants to access a larger volumes, including deeper soil layers (Horton and Hart, 1998; Shaver et al., 2000), which may explain the warming effects on deeper soils at our site.

4.2. Warming effects on soil CO_2 production and efflux

The average CO_2 flux across the experiment from both CGM and Licor-8100 A approaches are comparable to previously reported values for 5 year old Chinese fir plantations (Wang et al., 2017), and 40 year old Chinese fir plantations in the region (Li et al., 2016). The significant warming related increases in CO_2 production across the whole soil profile (Fig. 7) indicate that experimental warming affects the belowground processes that contribute to soil CO_2 efflux in tropical soils, in

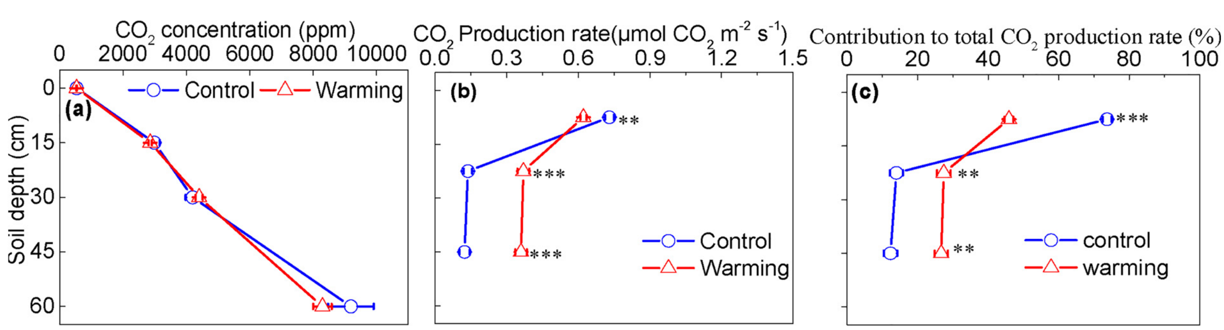

Fig. 6. The mean annual CO_2 concentration (a), the mean annual CO_2 production rate (b) and the contribution of mean annual soil CO_2 production rate (c) at each soil depth to the total CO_2 production rate in the warming treatment and the control. Error bars are standard errors (SE, n = 5). "**" and "***" indicate significant differences between control and warming treatment at $P < 0.01$ and 0.001 respectively.

Table 1
Soil physical and chemical parameters (including clay, silt, sand, pH, TC, TN, DOC, DON, NH_4^+-N and NH_3^--N) at the depths of 0–20 cm, 20–40 cm and 40–60 cm for the warming treatment and the control. Data are means ± standard error (n = 5). Different capital letters indicate significant differences between soil depths in the same treatment, and small letters indicate significant differences between the treatments at 0.05 significance ($P < 0.05$).

Treatment	Soil depth (cm)	bulk density (g cm^{-3})	Clay (%)	Silt (%)	Sand (%)	p H	TC (g kg^{-1})	TN (g kg^{-1})	DOC (mg kg^{-1})	DON (mg kg^{-1})	NH_4^+-N (mg kg^{-1})	NO_3^--N (mg kg^{-1})
CT	0-20	1.1 ± 0.1 Aa	14.4 ± 1.0 Ba	49.0 ± 2.2 Aa	36.6 ± 3.2 Ab	4.8 ± 0.1 Ba	12.3 ± 1.1 Aa	1.2 ± 0.1 Aa	9.9 ± 2.2 Aa	2.0 ± 0.5 Ab	5.5 ± 0.6 Aa	3.2 ± 0.5 Ab
	20-40	1.2 ± 0.0 Aa	14.8 ± 1.1 Ba	47.2 ± 2.4 Bb	38.0 ± 2.3 Aa	5.3 ± 0.1 Aa	3.3 ± 0.2 Ba	0.5 ± 0.1 Ba	4.0 ± 0.6 Ba	0.8 ± 0.5 Bb	5.8 ± 0.8 Aa	1.5 ± 0.4 Bb
	40-60	1.2 ± 0.1 Aa	15.5 ± 1.8 Aa	49.0 ± 1.5 Aa	35.6 ± 0.6 Bb	5.4 ± 0.1 Aa	3.0 ± 0.4 Ba	0.5 ± 0.0 Ba	4.0 ± 0.8 Ba	0.8 ± 0.7 Bb	6.1 ± 1.1 Aa	1.6 ± 0.7 Bb
W	0-20	1.1 ± 0.1 Ba	13.4 ± 1.1 Ba	45.5 ± 1.1 Bb	41.1 ± 1.7 Aa	4.7 ± 0.2 Ba	10.7 ± 2.0 Aa	1.1 ± 0.2 Aa	7.4 ± 0.3 Ab	5.9 ± 2.2 Aa	5.7 ± 0.6 Aa	7.9 ± 2.6 Aa
	20-40	1.2 ± 0.1 Aa	15.2 ± 0.7 Aa	49.5 ± 0.9 Aa	35.3 ± 1.2 Bb	5.1 ± 0.1 Aa	3.6 ± 0.4 Ba	0.6 ± 0.1 Ba	4.2 ± 0.6 Ba	6.0 ± 3.3 Aa	5.9 ± 0.3 Aa	7.5 ± 3.1 Aa
	40-60	1.4 ± 0.2 Aa	14.2 ± 2.0 Bb	46.4 ± 1.4 Bb	39.4 ± 2.5 Aa	5.2 ± 0.1 Aa	3.4 ± 0.7 Ba	0.5 ± 0.1 Ba	4.1 ± 0.9 Ba	5.3 ± 2.0 Aa	6.0 ± 0.9 Aa	7.2 ± 2.5 Aa

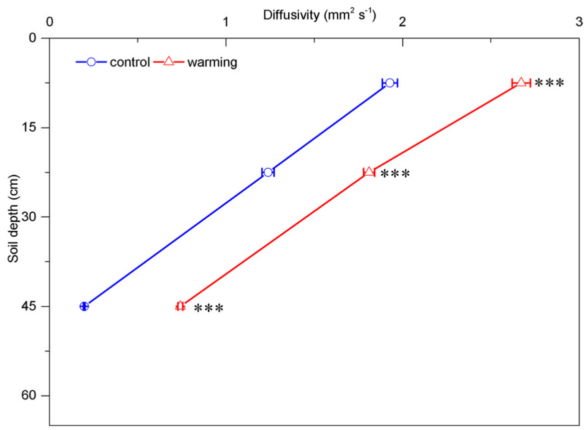

Fig. 7. The soil gas diffusivity at different soil depths in the warming and control treatments. Error bars are standard errors (SE, n = 5). "***" indicate significant differences between control and warming treatment at $P < 0.001$.

Table 2
Relative importance of the soil variables (include soil C, N content, pH, soil temperature, soil moisture, fine root production and fine root mortality) on the CO_2 production. The significance (*P* values) of the random forest model were 0.0001, 0.0001, 0.0001; and R^2 were 0.93, 0.98, 0.98 at the depths of 15 cm, 30 cm and 60 cm, respectively.

terms	15 cm		30 cm		60 cm	
	%IncMSE	*P*	%IncMSE	*P*	%IncMSE	*P*
Temperature	**15.1**	**0.002**	**14.0**	**0.002**	**16.0**	**0.002**
Moisture	**13.6**	**0.002**	**14.9**	**0.002**	**17.0**	**0.002**
The production of root	**22.1**	**0.002**	**12.5**	**0.012**	**12.0**	**0.006**
The mortality of root	9.8	0.164	**12.6**	**0.002**	**13.4**	**0.002**
DON	**13.5**	**0.002**	**14.6**	**0.004**	**11.8**	**0.004**
NO_3^--N	**13.0**	**0.002**	**13.9**	**0.002**	**12.2**	**0.004**
NH_4^+-N	**12.7**	**0.028**	3.1	0.441	9.7	0.246
DOC	**10.6**	**0.046**	9.5	0.377	7.3	0.421
TC	4.6	0.435	12.3	0.204	8.6	0.253
TN	3.8	0.521	11.2	0.244	9.1	0.277
pH	6.3	0.353	8.1	0.148	5.6	0.248

Notes: %IncMSE, Percentage of increase in mean square error. *P* = *P* values estimated by 9999 times of permutations. Values in bold are significant at $P < 0.05$.

support of our first hypothesis. Two meta-analysis studies have shown that warming generally increases soil surface CO_2 efflux by 12 to 27% (Wu et al., 2011; Wang et al., 2014), and so increases in our study system are consistent with warming responses observed in higher latitude systems.

There are a number of explanations for the warming related changes in our experiment. In this study warming increased gas diffusivity across the soil profile (Fig. 7), enhancing CO_2 transport along the soil profile. However, enhanced diffusivity alone cannot explain observed flux rate increases as soil CO_2 concentrations were similar across treatments (Fig. 3). Clearly, elevated soil surface and subsurface CO_2 production resulted from an increase in supply of C substrate in the warmed plots.

This increase has been attributed to the accelerated decomposition

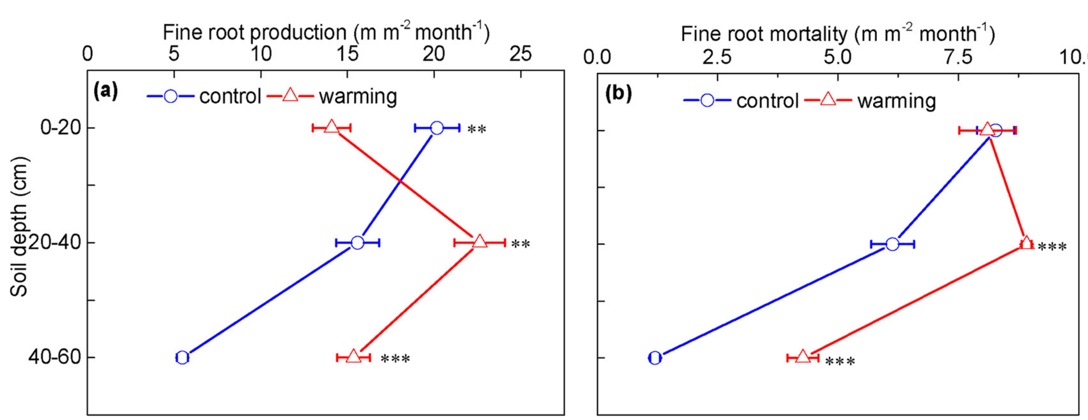

Fig. 8. The mean annual production and mortality of fine roots at different soil depths in the warming treatments and control. (a): Production of fine roots; (b) Mortality of fine roots. Error bars are standard errors (SE, n = 5). "**" and "***" indicate significant differences between control and warming treatment at $P < 0.01$ and 0.001, respectively.

of labile SOM stored in O horizon (Melillo et al., 2011; Frey et al., 2013). Our results from a subtropical forest site indicate that increases in soil surface CO_2 efflux also may be attributable to increases in CO_2 production in deeper soils, perhaps caused by increases in belowground inputs that can accompany warming (Litton and Giardina, 2008; Giardina et al., 2014). Because canopies were not warmed in our study, the source of increased available substrate required to drive higher CO_2 efflux is not as obvious. We suggest that there are three possible substrate sources for increased soil CO_2 production: 1) warming related changes to root activity; 2) increases in nutrient availability that drive changes in the canopy; and 3) accelerated decomposition of labile C.

4.3. Warming effects on fine roots, soil N, and DOC

Overall, our findings support our second hypothesis warming increases fine root turnover rate and activity in subsoil, with warming related increases in root growth, mortality and turnover likely providing a source of increased substrate for CO_2 production (Fig. 8), in line with previous findings that warming can significantly stimulate plant root growth (Andresen et al., 2010). Notably, warming can also reduce root growth and plant photosynthesis (Edwards and Richardson, 2004), possibly via reduced moisture (Dubrovsky et al., 1998). Moisture limitations in surface soils can drive plant roots to grow deeper into soils (Burgess et al., 2001; Schenk and Jackson, 2002; Yuan and Chen, 2010, which can explain the contrasting effects of warming on root activity in surface versus subsurface soils in our study. Interpreting our results is complicated by previous observations that direct soil warming by heating cables may increase root mortality (Edwards and Richardson, 2004), perhaps a direct temperature result or an indirect effect of reduced soil moisture (Dubrovsky et al., 1998). Exposure of Chinese fir to soil temperature above 35 °C more than two months (Fig. 1) may exceed fine root capacity to persist beyond thermal thresholds, also driving roots downward. Previous studies have also documented that root respiration increases with soil temperature (Burton et al., 2002; Schindlbacher et al., 2009), leading to lower fine root lifespans in warmer soils (Hendrick and Pregitzer, 1996; Eissenstat and Yanai, 1997). And so warming-related increases in subsurface root production and turnover in this study may have stimulated microbial activity in deep soil, and so soil CO_2 production (Hicks Pries et al., 2017).

A second substrate source driving higher CO_2 production may result from the indirect effects of warming on canopy photosynthesis via enhanced nutrient availability. Higher levels of soil NO_3^- and DON (Table 1), could following uptake and transport to leaves, stimulate canopy productivity (unpublished data), and in turn increase belowground C inputs (Ge et al., 2017). A previous meta-analysis on soil warming effects on temperate and boreal ecosystems have shown a strong positive effect of warming on soil N, including net N mineralization rate (52% increase) and net nitrification rate (32% increase) (Bai et al., 2013). Our subtropical study did not affect soil NH_4^+ concentration but did show 1.5 to 6.5 times' increases in NO_3^- and DON concentration, especially at deeper soils, in partial support of our third hypothesis.

Finally, a third source of increased substrate for CO_2 production could be an increase in labile C decomposition. The meta-analysis study by Lu et al. (2013) showed a 12.1% overall increase in DOC leaching loss under experimental warming. In contrast, we found that warming reduced DOC concentration at the 0–20 cm depth but did not affect DOC concentration in the depths of 20–40 and 40–60 cm, which partially contradicts our third hypothesis. This lack of an observed response could reflect the young age of the plantation. Alternatively, the lack of change in DOC concentrations in subsoils and the decrease in DOC concentrations in topsoils may result from increased cycling of DOC. Accelerated decomposition of labile C in surface detritus is an important component of warming related increases in soil CO_2 efflux (Melillo et al., 2002; Giardina et al., 2014).

Future work is required to more carefully quantify and disentangle the importance of these multiple drivers of increased CO_2 production. For example, laboratory and field studies suggest that soil respiration reaches the maximal rate in intermediate soil moisture levels, with low values at water deficiency or when the pore space needed for soil aeration is blocked, which can depress aerobic microbial activity (Luo and Zhou, 2010). The warming related reductions in surface soil moisture (Fig. 2b) as well as root production (Fig. 8a) would reduce substrate supply to microbes and inhibit SOM decomposition. Notably, warming did not stimulate CO_2 production in surface soils, which confirms previous work showing that reduced soil moisture and root activity are important drivers of CO_2 production in soils. In contrast, warming increased CO_2 production in subsoils despite strong moisture reductions (Figs. 1e, f, 2 b), highlighting the potential overriding importance of fine root activity as a driver of CO_2 production.

Our study has some limitations. First, this warming experiment was short-term, representing just one year of artificial warming. As has been demonstrated (Melillo et al., 2017), short-term responses may be ephemeral, and not indicative of long-term responses. Second, our study focused on the response of a forest early in stand development. Both above and belowground processes (plant productivity, above and belowground partitioning, stand water use) as well as forest structure and the accumulation of biomass, all change as tropical forests age from seedling to mature forest (Ryan et al., 2004). In Chinese fir, for example, the contribution of root respiration to total soil respiration can increase with age (Chen et al., 2016). Notably, while our results may not be representative of process rate responses for older forests, because seedlings were planted into warmed and control plots, we expect that our approach avoided exposing established vegetation to a large and unrealistic step increases in temperature – something encountered in most warming experiments of mature vegetation. We note that intensification of forest management practices means that larger areas of the tropics will occur as young plantations, and so our work provides a rare tropical dataset on the effects of warming on this increasingly important cover type.

5. Conclusion

Our subtropical study showed that warming elevated belowground C process rates, and these effects were strong in subsoil than topsoil. Organic C in subsurface tropical soil may be more vulnerable than in surface soils and thus global warming could exert a greater impact on young plantations in the subtropics and tropics than in temperate regions. Alternatively, the increased CO_2 production, especially in subsurface soils reflects accelerated cycling of labile C, with drying and warming related increases in gas diffusivity across the whole soil profile enhancing CO_2 efflux. The former interpretation suggests a positive feedback to future warming, while the later interpretation suggests a neutral or possibly negative feedback to future warming. Both of these interpretations are influenced by the effect of warming on N cycling. For example, accelerated NO_3^- leaching in humid subtropical ecosystems could cause or exacerbate N-limitations to forest growth in the tropics, or conversely, accelerated N cycling could result in higher productivity. Clearly more experimental warming research is needed to more accurately assess the likelihood of these distinct outcomes.

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