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Higher temperature accelerates carbon cycling in a temperate montane forest without decreasing soil carbon stocks

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ABSTRACT

Global warming is expected to accelerate the cycling of soil organic carbon (SOC) and the assimilation of new carbon, but the net effect of those counteracting accelerations and their ultimate effects on SOC are still uncertain. This hinders the prediction of long-term changes in biospheric carbon stocks and SOC-climate feedbacks. Here, we studied the long-term effect of temperature on carbon cycling across a 3.2 °C altitudinal temperature gradient in a temperate forest ecosystem in New Zealand. Across the gradient, soil respiration rates increased with increasing temperature from 9.0 to 10.4 tC ha^{-1} yr^{-1}, but SOC stocks down to 85 cm depth also tended to increase, from 154 to 176 tC ha^{-1}, albeit non-significantly ($P = 0.06$). This system was able to maintain higher soil respiration rates at higher temperatures without reducing SOC because the higher respiration rates were sustained by higher litterfall rates. Aboveground litterfall increased from 1.8 to 2.4 tC ha^{-1} yr^{-1} and estimated belowground C inputs increased from 7.2 to 8.0 tC ha^{-1} yr^{-1} along the temperature gradient. These higher fluxes were associated with significantly ($P < 0.05$) increased biomass at higher temperatures. As a direct measure of the effect of temperature on carbon cycling processes, we also calculated the turnover rate of forest litter which increased about 1.4-fold across the temperature gradient. This study demonstrates that higher temperatures along the thermal gradient increased plant carbon inputs through enhanced gross primary production, which counteracted SOC losses through temperature-enhanced soil respiration. These results suggest that temperature sensitivities of both plant carbon inputs and SOC losses must be considered for predicting SOC-climate feedbacks.

1. Introduction

Soils contain the largest carbon (C) pool in terrestrial ecosystems, with 1300–1500 GtC in the top 1 m of the world's soils (Harden et al., 2018) and 2400 GtC within the top 2 m, which is twice as much as atmospheric C (830 GtC) (Paustian et al., 2016) and forest biomass C (363 GtC) combined (Pan et al., 2011). The world's soils receive about 60 GtC yr^{-1} through aboveground litterfall and belowground C allocation, which is balanced by an approximately equal amount of C lost to the atmosphere through soil respiration (Houghton, 2007). As soil respiration rates are strongly regulated by temperature, it is assumed that rising temperatures will accelerate the rate of soil organic carbon (SOC) decomposition which could cause a decrease in soil C stocks, thus accelerating global warming (Kirschbaum, 2000a; Davidson and Janssens, 2006; Bond-Lamberty and Thomson, 2010). Crowther et al. (2016), for example, used a business-as-usual emissions scenario and projected a net loss of 55 (±50) GtC from the top 10 cm of the world's soils by 2050, which would add approximately 12–17 % to the projected

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Abbreviations: MAT, mean annual temperature; NPP, net primary productivity; SOC, soil organic carbon; Q_{10}, temperature sensitivity of soil organic carbon decomposition.

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anthropogenic CO_2 emissions over this period (Riahi et al., 2011; Ballantyne et al., 2015).

However, some studies have shown that warming has no, or even positive effects on soil C stocks (Lu et al., 2013; Sistla et al., 2013; Blagodatskaya et al., 2016). These mixed results could be attributed, in part, to interacting factors, with concomitant changes in net primary productivity (NPP) being particularly important (Kirschbaum, 2000a; Rustad et al., 2001; Wu et al., 2011). This is illustrated in Fig. 1.

If one considers only the effect of temperature on specific decomposition rate (Fig. 1A – hypothesis 1), then any temperature increase would increase the SOC loss rate until relevant pools have shrunk to a size where feedbacks from that reduced pool size force a reduction in the SOC loss rate (e.g. Jenkinson et al., 1991). The system would eventually reach a new steady state at the higher temperature, with SOC gain and SOC loss again in balance but at a lower pool size. That would correspond to the latitudinal pattern of SOC stocks across the world and constitute a positive feedback effect that could amplify future climate change. However, if temperature stimulates not only SOC losses but NPP as well (Fig. 1B – hypothesis 2), then the temperature-induced stimulation of both SOC gains and SOC losses could cancel out (e.g. Rustad et al., 2001; Wu et al., 2011). With increasing temperature, soil respiration rates could be increased, but pool sizes could remain unchanged. In that case, the world's SOC pools might not change with warming, and there would be not positive or negative SOC-climate feedback effects (Smith et al., 2008). Therefore, further studies on the long-term effects of warming on SOC stocks are needed to reduce the uncertainties associated with the prediction of future SOC–climate feedback.

Laboratory and field experiments that impose artificial warming generally cannot be run long enough for determining the long-term response of SOC stocks to warming. This is due to the long mean residence time of slowly cycling SOC pools, making it difficult to forecast changes in stable SOC pools (Powlson, 2005). To overcome that problem, some investigations have used a space-for-time substitution approach to study the long-term warming effects on SOC. However, these studies are often confounded by variables other than temperature (Conant et al., 2011). In an attempt to overcome these difficulties, Giardina et al. (2014) investigated changes in the SOC pools and fluxes along a temperature gradient (from 13 to 18 °C) in the tropical wet montane forest of Hawaii, where the factors other than temperature that can affect ecosystem processes (e.g., soil, vegetation and plant-available soil moisture) were relatively similar. They reported no significant effect of temperature on either SOC stocks or the turnover of old SOC fractions, with warmer sites having higher belowground C inputs and faster cycling of incoming plant-derived C but found no evidence of warmer temperatures having a consistent impact on SOC stocks, in line with hypothesis 2 (Fig. 1B).

Mount Taranaki in New Zealand offers an opportunity to further test hypothesis 2, as it has a strong temperature gradient, with other potential drivers of C dynamics being either similar or non-limiting. Compared to the Giardina et al. (2014) study from Hawaii, our site on Mt. Taranaki covered a lower temperature range, with mean annual temperature (MAT) of 7.3–10.5 °C and is covered by temperate rainforest (Clarkson, 1986) instead of tropical montane wet forest in Hawaii (MAT: 13–18 °C). The studies were functionally comparable, however, in that they both covered natural temperature gradients with temperature as the key variable controlling factor of carbon dynamics, while other important factors were either similar across the gradient, such as soil types, or non-limiting, such as water availability. Therefore, the objectives of this study were to evaluate (i) whether temperature stimulates both NPP and soil C losses, and (ii) if that is the case, to what extent C inputs and outputs cancel out. The final goal was to improve our global understanding of soil C-climate feedbacks.

2. Materials and methods

2.1. Site description

The study was conducted in a mature native forest on the eastern flank of Mt. Taranaki, North Island, New Zealand. Investigation and sampling were carried out at four elevations ranging from 525 to 1025 m above sea level (asl) with an altitude increment of *ca* 150 m, corresponding to mean annual temperatures of 7.3 °C (T7), 8.2 °C (T8), 9.1 °C (T9) and 10.5 °C (T10), respectively (Supporting Information, Fig. S1 and Table S1). Mean annual precipitation exceeded 3000 mm yr^{-1} at all sampling sites, gradually increasing with elevation (from 3400 mm yr^{-1} at T10 to 6531 mm yr^{-1} at T7). All sampling sites have the same parent material and native evergreen broadleaf trees (>80 % with kamahi (*Weinmannia racemosa* L.f.) and mahoe (*Melicytus ramiflorus* J.R and G. Forster), and soil moisture was considered to be non-limiting for plant growth at all sites. The soil was formed on andesitic tephra from the Burrell lapilli eruption that occurred in 1655 CE (Aitken et al., 1978). It is classified as an alu-andic Andosol according to the World Reference Base system (World Reference Base for Soil Resources, 2015). The native forest was assumed to be in a steady state in terms of soil C stocks after growing for over 400 years since the last eruption without major disturbance (Knowles and Beveridge, 1982). There is no documented evidence of any major damage caused by natural (e.g., floods, windstorms, animal pests or widespread diseases) or human disturbance (e.g., logging) that could have resulted in significant changes to the forest's structure.

2.2. Aboveground and belowground live biomass C

At each elevation, canopy trees were surveyed within a 400 m^2 area.

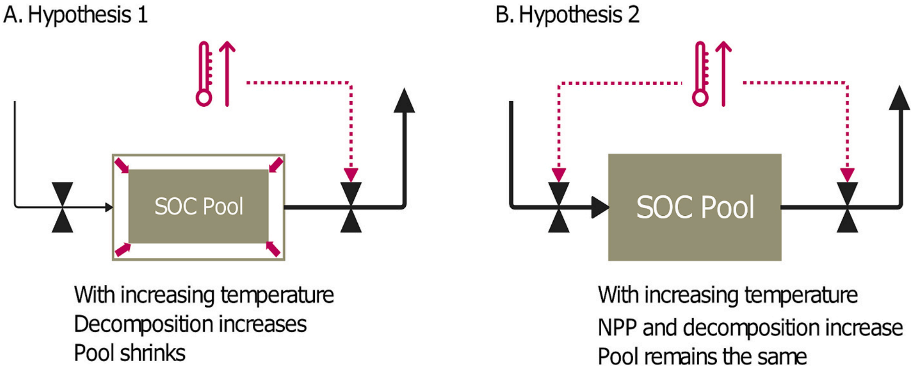

Fig. 1. A conceptual diagram of SOC pools as influenced by increasing temperature. Shown are hypothesis 1, in which an increase in temperature stimulates only specific decomposition rate (as shown by the thicker black line on the right-hand side) (A) and hypothesis 2, in which an increase in temperature equally stimulates NPP and specific decomposition rate (as shown by the ticker black lines on both sides), leading to compensating effects on biospheric carbon-stock pools. Adapted from Kirschbaum (2000a).

Kamahi (*Weinmannia racemosa* L.f.), tawa (*Beilschmiedia tawa* (A. Cunn) Kirk)) and mountain totara (*Podocarpus cunninghamii* Hooibr. ex Endl) dominated the canopy, ranging in height from 20 to 30 m. Mahoe (*Melicytus ramiflorus* J.R and G. Forster) dominated the understorey trees, with a height range of 10–15 m. Tree ferns (*Hymenophyllum* spp. Sm) were prevalent at the two highest sites, where the weather conditions were colder and wetter. Aboveground biomass C was estimated using allometric equations developed by Beets et al. (2012) for indigenous tree species in New Zealand. The allometric equations differentiate between stems with a diameter at breast height (1.4 m above the ground) of ≥0.10 m and < 0.10 m. Root biomass C, B_r, was estimated as:

$$B_r = 0.489\, {B_s}^{0.890} \tag{1}$$

where B_s is the estimated above-ground shoot biomass, and the parameters were given in the systematic global review of root biomass by Mokany et al. (2006). For all targeted trees, the diameter at breast height was measured with a diameter tape (Larjavaara and Muller-Landau, 2013).

2.3. Forest floor biomass C

At all sampling elevations, materials from the forest floor were collected every 2 months from 4 square subplots (0.5 m × 0.5 m) within the 400 m^2 plots. The collected forest floor materials were dried in an oven at 65 °C to a constant weight. The materials were then separated into leaf, twig, branch and bark material, and each component was weighed. The C content of each component of the forest floor material was analysed using an Elementar Vario MACRO analyser (Hanau, Germany).

2.4. CO_2 efflux from the soil surface and intact soil cores

At each elevation, four static chambers made from polyvinyl chloride collars (diameter: 230 mm; height: 250 mm) were inserted about 50 mm into the ground to collect soil CO_2 fluxes. At sampling times, the chambers were closed by a lid with a batten to turn and lock the lid in position. Gas sampling was carried out after 0, 30 and 60 min with four replicates at each site. CO_2 concentrations were measured with a gas analyser fitted with a CO_2 transducer (Analytical Development Co, Hoddesdon, UK) using N_2 as a carrier gas at a flow rate of 35 mL min^{-1}. The gas analyser was calibrated with a 0.5 % CO_2 β-standard (BOC Ltd., Auckland, New Zealand), and the linear signals over the standard range were recorded with an HP 3396 A integrator. CO_2–C efflux from the soil surface (F_s) was calculated according to the following equation.

$$F_s = \alpha_v \times V_c / V_{m,T} / S_c \times 12 \tag{2}$$

where α_v is the slope of the CO_2 concentration vs. sampling time curve; V_c and S_c are the volume and the bottom surface area of the chamber, respectively; $V_{m,\ T}$ is the molar volume of an ideal gas at the corresponding air temperature T during the sampling interval; 12 is the molar weight of C (g mol^{-1}). Soil CO_2 efflux was measured every month for 1 year (April 2019–March 2020). Air temperature was recorded in situ every 30 min with a Tinytag Plus 2 data logger (Gemini Data Loggers Ltd., West Sussex, UK).

The field measurements of F_s combine autotrophic respiration from roots and heterotrophic respiration from soil organic matter decomposition. We also evaluated soil CO_2 efflux from the decomposition of bulk soil organic C by incubating intact soil cores under 5 °C and 15 °C for 330 d in the laboratory. Further details of the incubation experiment are provided in the supporting information.

2.5. Aboveground C input

Aboveground C input (F_{AC}) primarily consisted of litterfall, which was collected monthly, including dead leaves and small branches <10 cm in diameter. Five litter traps were placed at each sampling site. One trap had a collection surface of 1 m × 1 m, and the other four were 0.4 m × 0.6 m. The litterfall biomass was dried at 65 °C to a constant weight, and litterfall C was calculated by multiplying the measured weight by the C contents of each litterfall component. Coarse woody debris was estimated to be ≤5 % of F_{AC} at each sampling site and was assumed to be at a steady state. Annual aboveground C input rate was calculated by summing monthly litterfall rates over a whole year.

2.6. Belowground C allocation

Total belowground C allocation is defined as the annual total C allocated belowground to grow and maintain roots, supply mycorrhizae and other symbionts, and generate root exudates (Giardina et al., 2004). The forest at the sampling sites was considered to be in a steady state. Under this assumption, the amount of C that enters the annual above- and belowground pools must be equal to the annual C loss:

$$F_S = F_{AC} + F_{BC} \tag{3}$$

Thus,

$$F_{BC} = F_S – F_{AC} \tag{4}$$

where F_S is the CO_2–C efflux from the soil surface, F_{AC} is the C input from litterfall and F_{BC} is the C input from belowground sources. This approach is coupled with the assumption that annual changes in soil C stocks are negligible in undisturbed forests (Raich and Nadelhoffer, 1989; Nadelhoffer et al., 1998; Gower et al., 1996). Carbon loss through leaching was assumed to be minor, as supported by the finding of Sparling et al. (2016) that the mean annual C leaching rates of New Zealand Andosols were 13 to 29 kg C ha^{-1} yr^{-1}.

2.7. Soil C contents and stocks

Soil samples were collected at four sites within a 400 m^2 plot at each elevation using a soil core (25-mm in diameter) at four different soil depths (0–10, 10–30, 30–50, and 50–85 cm). Soil C contents were measured using the Elementar analyser previously described. Total soil C stocks (in tC ha^{-1}) at fixed depths were calculated by considering the soil C content, bulk density, and soil depth. Total soil C stocks at these depths were calculated after correcting for the presence of coarse fragments (> 2 mm), following Schwager and Mikhailova (2002) as follows:

$$TC_s = TC \times \rho \times D \times (1 - \delta_{2mm}) \times 0.1 \tag{5}$$

where TC_s represents the C stocks of a specific soil layer (TC ha^{-1}), ρ represents the soil bulk density (g cm^{-3}), D represents the thickness of the soil layer (cm), and δ_{2mm} represents the proportion of coarse fragments on a volume basis (>2-mm mesh) (%). We estimated soil C stocks at the different depths (0–10, 10–30, 30–50, and 50–85 cm), as needed to determine the cumulative soil C stocks at 0–10, 0–30, 0–50, and 0–85 cm on an equivalent soil mass basis using the cubic spline method of Microsoft Excel (Wendt and Hauser, 2013). For each of the three top depth intervals (0–10, 0–30, and 0–50 cm), the average of the corresponding cumulative soil masses across sites was considered. For the whole soil interval (0–85 cm depth), the minimum soil mass across sites was considered instead, so that that the C stocks calculated via the cubic spline method could fall within the interpolation zone (Wendt and Hauser, 2013). The cumulative soil masses at specific depths considered were as follows: 0–10 cm = 469 t ha^{-1}; 0–30 cm = 1800 t ha^{-1}; 0–50 cm = 3215 t ha^{-1}; and 0–85 cm = 4613 t ha^{-1}.

2.8. Data analysis

Statistical analyses were carried out using the IBM SPSS Statistics version 25.0 (IBM Corp, Armonk, New York, USA). One-way ANOVA with Tukey's tests were performed to find significant differences (at $P <$

0.05). Two-way ANOVA were conducted to examine the effects of MAT, soil depth and their interactions on soil total C contents and cumulative soil C stocks. Pearson's correlation was used to evaluate the linear relationship between two variables.

3. Results

3.1. Soil organic C contents and stocks

There was no consistent relationship between total SOC contents at different depths and mean annual temperature (Fig. 2A). At 0–10 cm soil depth (the topmost points in Fig. 2A), there were no significant differences ($P > 0.05$) in total SOC contents between the four sites. At 10–30 cm, the SOC contents of T7 and T8 were significantly greater than those of T9 and T10. At depths of 30–50 and 50–85 cm, total SOC contents at T10 were significantly greater than those at the other sites. Total cumulative soil C stocks calculated on an equivalent soil mass basis of 4613 t ha^{-1} tended to increase with increasing temperature, ranging from 153.6 ± 11.7 to 176.4 ± 10.4 tC ha^{-1} between T7 and T10, but these differences were not significant ($P = 0.06$) across the studied sites (Fig. 2B).

3.2. Net primary production and C input fluxes

T10 had the largest aboveground biomass C of 214 ± 13 tC ha^{-1}, which was significantly ($P < 0.05$) larger than the biomass of T8 and T7 with mean values of 177 ± 10 and 162 ± 12 tC ha^{-1} respectively (Fig. 3A). In contrast, forest-floor C stocks decreased with increasing temperature, albeit significantly only between T7 and T10 ($P < 0.05$) (Fig. 3B).

Annual aboveground C input rates (Fig. 4A) ranged between 1.8 and 2.4 tC ha^{-1} yr^{-1}. This resulted in a strong positive correlation between the annual sum of litterfall and mean annual temperature of the sites ($r = 0.96$, $P = 0.035$) (Fig. 4A). Based on measured forest floor mass and litterfall rate, we estimated the mean residence time of forest litter (i.e. forest floor biomass C/ litterfall) to decrease by 24% from the coolest to the warmest site (Fig. 4B). Accordingly, the temperature sensitivity (Q_{10}) of the forest floor turn-over rate was estimated to be about 2.44. Annual belowground C fluxes through plant allocation was estimated as the difference between total soil respiration and litterfall. It also tended to increase with increasing temperature ($r = 0.98$, $P = 0.021$; Fig. 4A).

3.3. Specific decomposition rates and C output fluxes

Soil respiration rates followed a clear seasonal pattern (Fig. 5B) with highest rates in summer (from December to February), when temperatures were highest (Fig. 5A). Rates were lowest in the coldest months (May and September). Soil respiration rates from all four sites conformed to an identical logarithmic relationship with temperature over a wide temperature range throughout the year ($R^2 = 0.82$, $P < 0.05$, Fig. 5C). Annual cumulative soil respiration for the four sites was strongly positively correlated with temperature ($r = 0.99$, $P = 0.01$) (Fig. 5D).

To evaluate the temperature sensitivity of bulk SOC decomposition rates, we incubated intact soil cores collected at various soil depths (0–5, 10–15, 20–25, and 35–40 cm), at two different temperatures in the laboratory (methodology described in SI). Under both 5 °C and 15 °C, the decomposition of SOC as a proportion of total SOC (SOC-normalised efflux) decreased with increasing temperature (i.e., lower at T10 than at T7) and soil depth ($P < 0.001$, Fig. 6A and B). The temperature sensitivity (Q_{10}) of decomposition also decreased slightly, but significantly, with soil depth ($P < 0.001$), whereas it did not differ significantly between the four sampling sites ($P = 0.11$, Fig. 6C).

3.4. Carbon budgets

Fig. 7 schematically summarises the key C stocks and fluxes of the forest ecosystem for T7 and T10. C stocks in aboveground biomass were 162 ± 12 tC ha^{-1} at T7 and 214 ± 13 tC ha^{-1} at T10. Similarly, belowground biomass (root biomass) increased from 45.3 ± 2.3 to 58.0 ± 1.4 tC ha^{-1}. Litterfall concomitantly increased by 29 % from 1.8 ± 0.2 to 2.4 ± 0.1 tC ha^{-1} yr^{-1}, whereas belowground carbon influx increased by 15 %, from 7.2 ± 0.1 to 8.0 ± 0.4 tC ha^{-1} yr^{-1}. Soil respiration increased from 9.0 ± 0.8 tC ha^{-1} yr^{-1} at T7 to 10.4 ± 0.4 tC ha^{-1} yr^{-1} at T10. Using Eq. 4, we estimated belowground C input from plant roots to be the largest contributor to total soil respiration, accounting for about three-quarters of total soil CO_2 efflux, with litterfall contributing the other quarter. Although SOC stocks tended to increase from T7 to T10, there was no significant difference between the two sites. Therefore, we displayed the average value of soil C stocks of the four elevations (162 tC ha^{-1}) in Fig. 7. The forest floor C stocks, which represent the smallest C pool considered, showed a different pattern, declining from 3.2 ± 0.3 tC ha^{-1} at T7 to 2.9 ± 0.3 tC ha^{-1} at T10.

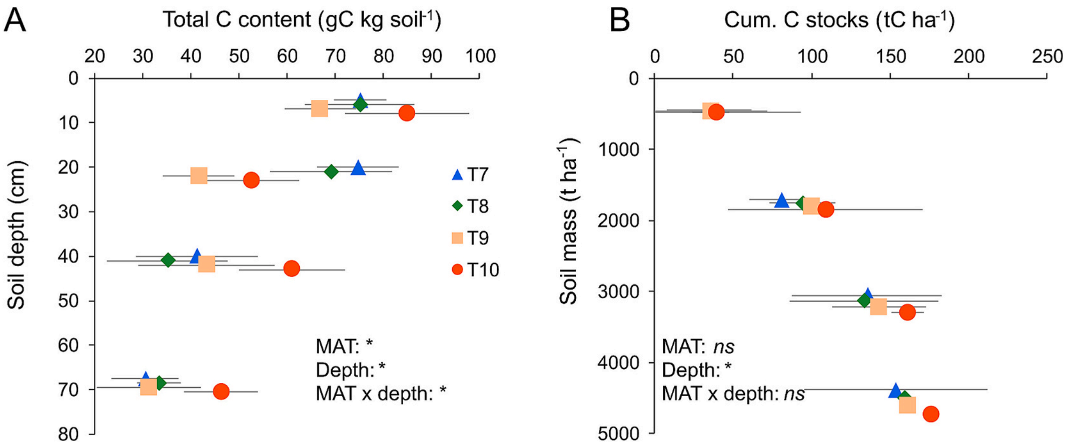

Fig. 2. Soil organic carbon contents and stocks. (A) Total organic carbon contents by soil depth (10, 30, 50, 85 cm); and (B) cumulative soil C stocks down to 85 cm (469, 1800, 3215, 4613 t ha^{-1}), expressed as a function of equivalent soil mass. Note the data points are jittered by soil depth/mass to avoid overlapping. MAT stands for mean annual temperature; T7, T8, T9 and T10 indicate the site with a MAT of 7.3, 8.2, 9.1 and 10.5 °C, respectively. * and *ns* indicate significant and non-significant differences, respectively, according to a two-way ANOVA ($P < 0.05$). Error bars represent the 95 % confidence interval of the mean ($n = 4$).

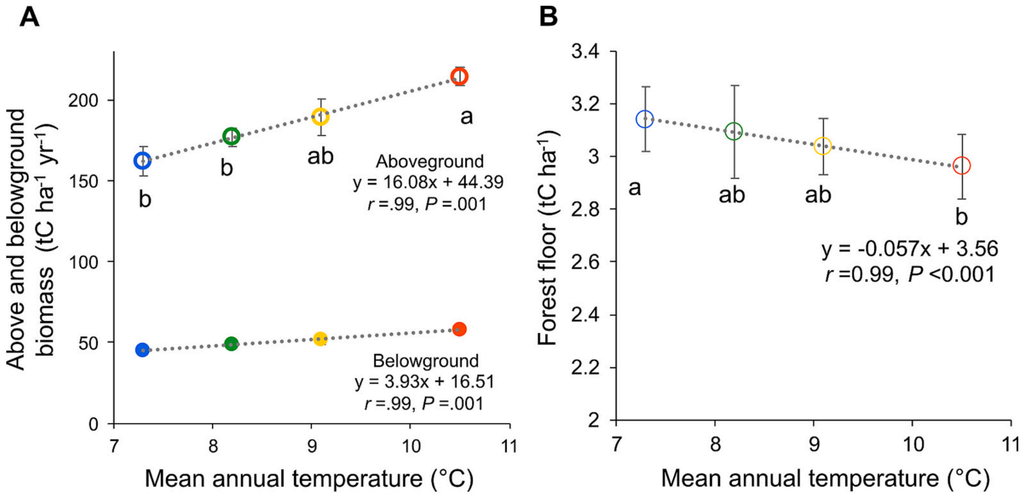

Fig. 3. Biomass and forest floor carbon stocks. (A) Aboveground biomass and belowground biomass C, and (B) forest floor C stocks at the four sites with different mean annual temperatures. Different letters denote significant difference in total biomass ($P < 0.05$) among sites according to one-way ANOVA followed by Tukey's test. Error bars represent the 95 % confidence interval of the mean ($n = 4$ for biomass and $n = 6$ for forest floor).

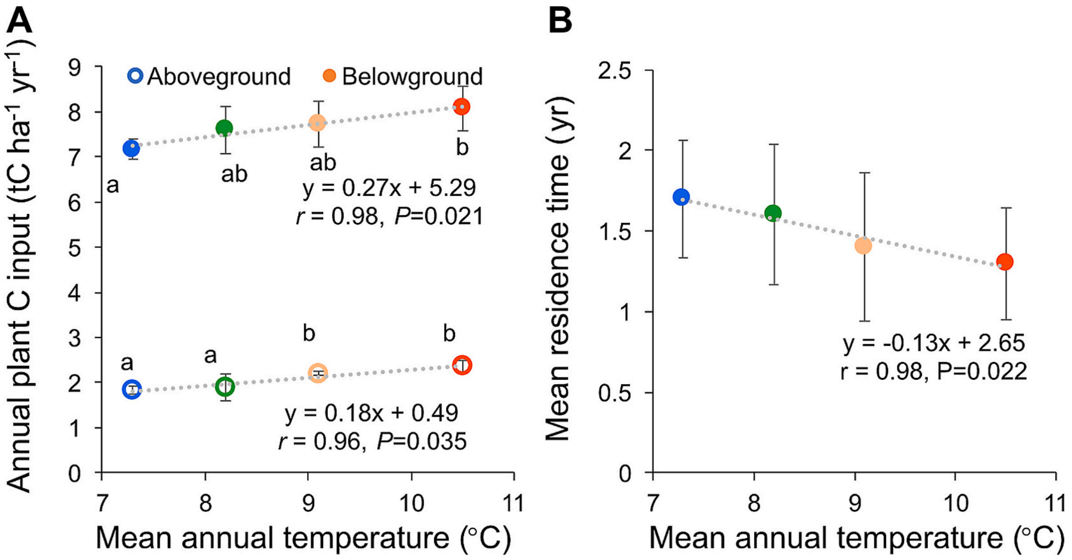

Fig. 4. Annual plant carbon input and mean residence time of forest litter. (A) Total annual aboveground and belowground carbon input as a function of mean annual temperature; (B) The mean residence time of forest floor as a function of mean annual temperature. Error bars represent the 95 % confidence interval of the mean ($n = 5$).

4. Discussion

4.1. Carbon inputs to the system increase with temperature

The annual below- and above-ground C inputs together increased by 15.6 % (1.4 tC ha^{-1} yr^{-1}) between the sites with lowest (T7) and highest temperature (T10; Fig. 7), in line with hypothesis 2 (Fig. 1B). Similar findings – that is, the increase in NPP with temperature – have been observed along elevation gradients (Joshi et al., 2003; Sheikh et al., 2009) and at a global-scale (e.g. Lieth, 1973; Kirschbaum, 2000b; Wu et al., 2011; Chen et al., 2013). Higher temperature could enhance enzyme activity and photosynthetic rates, thus leading to greater biomass growth rate, reflected in greater standing aboveground biomass (Fig. 3A)(Luo et al., 2009; Zhang et al., 2013; Baig et al., 2015). Root growth can also be enhanced by warmer temperatures through an increase in the metabolic activity of root cells and by promoting the development of lateral roots, thereby generating greater root biomass (McMichael and Burke, 1998; Puhe, 2003; Repo et al., 2004). Additionally, forest productivity at colder sites may have also been reduced by greater cloud cover, which reduced irradiance and photosynthesis (Mulkey et al., 1996). The higher plant productivity of the forest system at higher temperature in turn, led to enhanced rates of litterfall and belowground C flux rates (Pietikäinen et al., 2005; Koch et al., 2007).

4.2. Soil CO_2 efflux increases with temperature and balances out soil C inputs

A key finding of this study is that the increase in measured soil respiration between the sites with lowest (T7) and highest temperature (T10) was ca. 1.4 tC ha^{-1} yr^{-1} (Fig. 6), which balanced the total input flux of ca. 1.4 tC ha^{-1} from above- and belowground biomass. That is, both C gains and C losses were larger at the warmer sites and they cancelled out, which explains the lack of significant change in SOC stocks with temperature. Thus, in this specific ecosystem and pedoclimatic conditions, the net impact of the proven hypothesis 2 (Fig. 1B) – i.

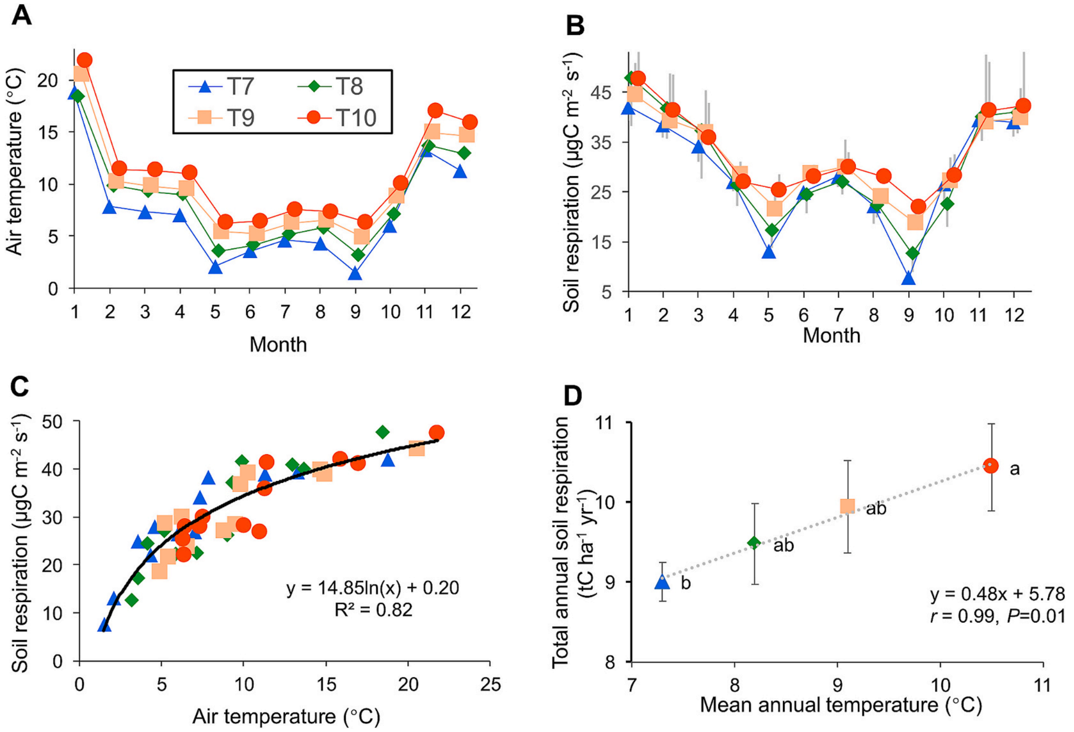

Fig. 5. Soil respiration rate and its relationship with air temperature. (A) Monthly mean air temperature; (B) Soil respiration; (C) The relationship between soil respiration and monthly mean air temperatures over all sites and measurement periods; (D) Annual cumulative soil respiration at each elevation. T7, T8, T9 and T10 indicate the site with a MAT of 7.3, 8.2, 9.1 and 10.5 °C, respectively. Note the data points are jittered by month in plots A and B to avoid overlapping. Different lowercase letters in panel D denote significant differences according to a one-way ANOVA followed by Tukey's test ($P < 0.05$). Error bars represent the 95 % confidence interval of the mean ($n = 4$).

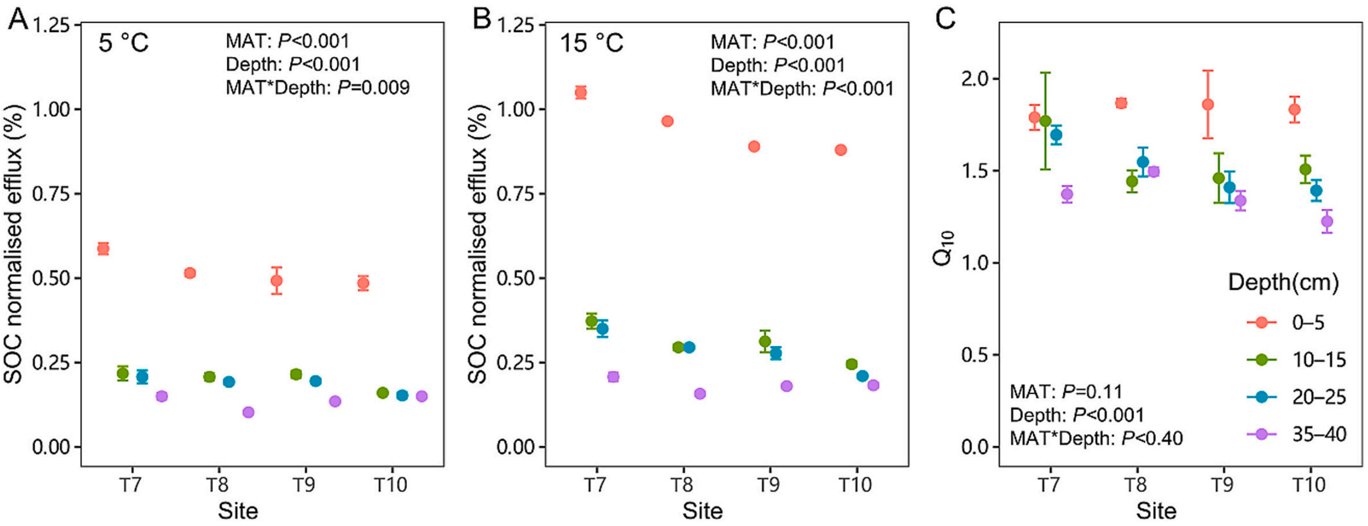

Fig. 6. Decomposition of bulk soil organic C in intact soil cores collected at different soil depths (0–5, 5–15, 20–25, and 35–40 cm). Samples were incubated at 5 °C and 15 °C for 330 d. Cumulative CO_2-C efflux as a fraction of total soil organic C at (A) 5 °C and (B) at 15 °C; and (C) temperature sensitivity (Q_{10}) of the decomposition rates. MAT stands for mean annual temperature; T7, T8, T9 and T10 indicate the site with a MAT of 7.3, 8.2, 9.1 and 10.5 °C, respectively. Note the data points are jittered by site to avoid overlapping.

e., with increasing temperature, both NPP and soil respiration rates increase – is an unchanged size of the SOC pool.

The turnover rate of forest litter increased about 1.3-fold from the coolest to the warmest site, with an estimated Q_{10} of about 2.44 (Fig. 4B). This level of stimulation falls within the range of Q_{10} values reported for organic matter decomposition (Kirschbaum, 2000a; Salinas et al., 2011). Monthly soil respiration measurements increased very sharply from the lowest temperatures of about 5 °C to 10–15 °C, with more moderate further increases for further increasing temperatures. This temperature response curves showed a more logarithmic shape as the temperature increased, which differs from the exponential relationship between respiration and temperature often observed in previous warming experiments (i.e., Kirschbaum, 2000a). This difference response pattern may be related to changing substrate availability over the season, with variable litterfall rates (see Fig. 4) and depletion of readily decomposable substrate over periods with conditions that are

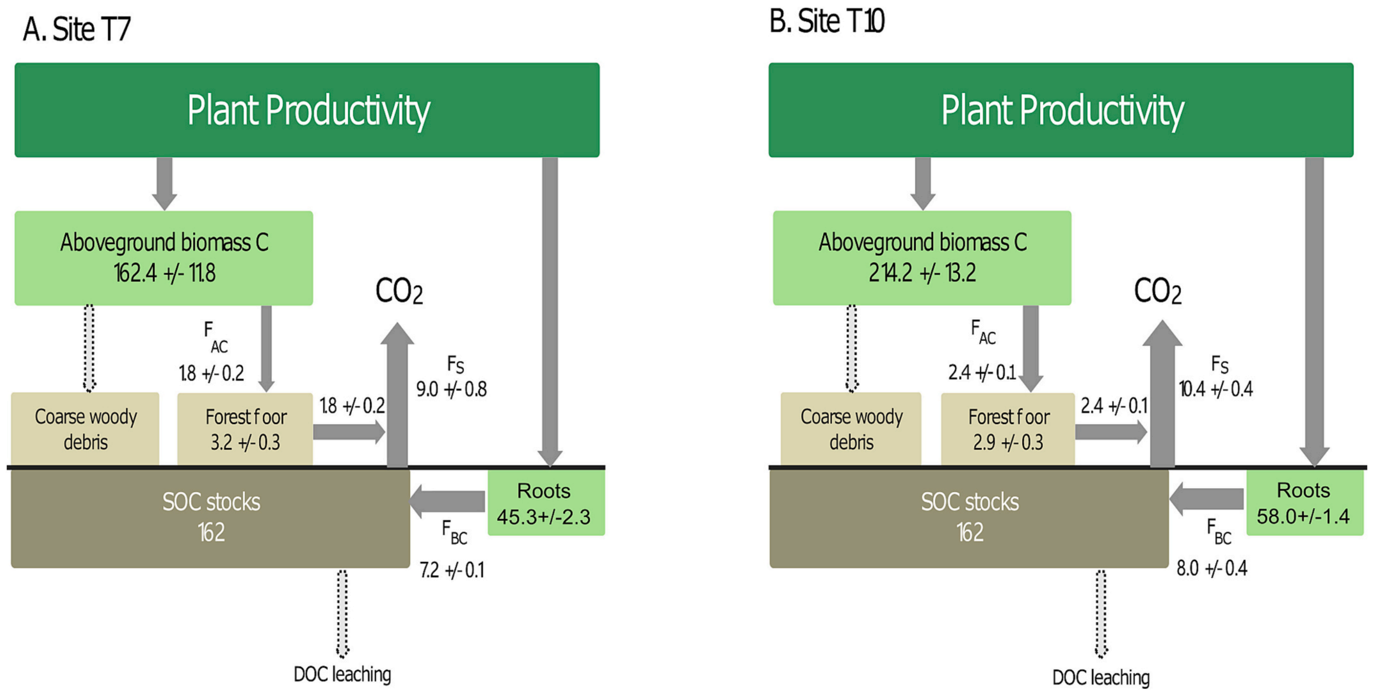

Fig. 7. A summary of the changes in soil C cycling and stocks across the thermal gradient in a mature native forest ecosystem. The generation of new coarse woody debris and leaching of dissolved organic C (DOC) are shown with dashed arrows to indicate that they are negligible. Fluxes (tC ha^{-1} yr^{-1}) are in arrows and stocks (tC ha^{-1}) in boxes. Note soil organic C stocks are shown as the mean of the four sites as there no significant difference between the sites. Abbreviations: F_{AC}, aboveground C input (i.e. litterfall C); F_s, CO_2–C efflux from the soil surface; F_{BC}, C input from belowground sources.

favourable for rapid decomposition.

Our laboratory incubations of the decomposition of bulk SOC from different soil layers and sites helped understand the response of SOC availability to artificial heating. When they were incubated at the same incubation temperature in the laboratory, samples from warmer sites lost slightly less carbon than those from cooler sites (Fig. 5), indicating a reduction in SOC availability with increasing temperature. This statement is supported by our previous observation that a greater extent of SOC protection by reactive minerals as indicated by a larger value of hydrofluoric acid extractable SOC fraction from warmer sites (Siregar et al., 2024). Recent papers have proven that organo-mineral associations reduce the temperature sensitivity of SOC decomposition by decreasing SOC availability (Georgiou et al., 2024).

Furthermore, our data were expressed against air temperature, not soil temperature, as we had no permanent soil temperature gauges installed. The lag between air and soil temperatures may modify the shape of the temperature response curve of soil respiration (see Fig. S3 for an illustration). More specifically, soil temperatures at depths are lower than air temperatures in summer and greater in winter (Seward et al., 2013). Accordingly, as the functionally relevant soil temperature is lower than air temperature in summer, a steep soil respiration vs soil temperature relationship should be transformed into a shallow and more logarithmic soil- respiration vs air temperature relationship (Fig. S4). The opposite pattern could pertain over the winter months. (Zhang et al., 2018).

4.3. Higher temperatures did not cause a loss of soil C stocks

Along the thermal gradient, we observed that soil C stocks were not significantly different between sites (Fig. 1B), despite the associated increase in soil respiration. This was attributed to C gain both above- and belowground as well as carbon losses from soil respiration being higher at the warmer sites. The enhanced C inputs counteracted the C loss from soil respiration, resulting in no significant change in C stocks along the thermal gradient. Our findings were very similar to those of Giardina et al. (2014). Both studies found that increasing soil respiration at higher temperature did not decrease soil C stocks because higher soil respiration rates were matched by similarly stimulated carbon input rates by higher temperature. Similarly, Ziegler et al. (2017) also found that along a latitudinal transect, carbon fluxes increased with mean annual temperature without changing soil carbon stocks. Other studies, like those of Conant et al. (1998) and Garten and Hanson (2006), reported different patterns but in their studies, vegetation types and soil moisture differed along the elevation gradients so that any observed differences in pools and fluxes could not be related solely to temperature differences. Instead, the differences in environmental variables other than temperature confounded the effects of warming on soil C cycling.

Our study was broadly consistent with temperature effects seen in previous soil warming studies (Kirschbaum, 2000a; Rustad et al., 2001; Soong et al., 2021). Even though most soil-warming experiment primarily heat the soil with less direct effect on the whole ecosystem, most prior studies still reported increases in net primary productivity, litterfall, and belowground C allocation (Rustad et al., 2001) that could negate SOC losses from increased soil respiration rates. If soil respiration is stimulated by warming and plant C inputs remain constant, soil C must inevitably be lost. However, if both carbon losses and carbon gains increase with warming, then soil carbon can remain the same. Soil warming also leads to transient effects (e.g. Kirschbaum, 2004; Eliasson et al., 2005) that change over the length of the experiment and makes it difficult to extrapolate findings to longer-term responses. In contrast, our experiment focused on the long-term effects of warming on soil C stocks.

5. Conclusions

Our results clearly showed that elevated temperatures accelerated both soil C inputs and outputs in the forest ecosystem of Mt. Taranaki. The increased C losses were balanced by increased C gains, resulting in no significant change in SOC stocks along the thermal gradient. These results add to the global dataset of the effects of elevated temperature on

SOC stocks from the Southern Hemisphere, which is one of the most underrepresented regions in the global database. Our data corroborate findings from most field warming experiments that long-term warming might not significantly change SOC stocks, provided that net primary production changes as much as the enhanced organic matter decomposition.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use generative AI and AI-assisted technologies in the writing process.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geodrs.2024.e00889.

Data availability

All data generated during this study are presented in the main text and the supporting information and are available upon request from the authors.

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