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Warming increases the relative change in the turnover rate of decadally cycling soil carbon in microbial biomass carbon and soil respiration

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Decadally cycling soil carbon (dSOC) is the main component of the terrestrial soil carbon (C) pool. The response of dSOC to warming largely determines the feedback between climate warming and the C cycle. However, there is a lack of investigations about the effect of warming on the relative change in turnover rate (RCT) of dSOC and annually cycling SOC (aSOC) in dissolved organic carbon (DOC), microbial biomass carbon (MBC) and CO₂. We clarified this issue by incubating two C₃-C₄ vegetation switch soils (23 years switch, HA soil and 55 years switch, GG soil) at 20°C and 30°C in the recently improved continuous airflow CO₂ trapping system for 1 year. Warming increased the contribution of dSOC (C₃-C) by 21% (soil HA) and 8% (soil GG) in MBC, and 38% (soil HA) and 15% (soil GG) in CO₂, while only 2%–3% increase in DOC at the final stage of the incubation. Furthermore, warming increased the RCT in MBC and CO₂ by 5.3- and 4.1-fold, respectively, but had no significant influence on the RCT in DOC, indicating that soil microbes may be an important engine to accelerate dSOC-derived CO₂ emission in a warming world.

KEYWORDS

warming, decadally cycling soil organic carbon, 13 C natural abundance, microbial biomass, terrestrial ecosystems

Introduction

Soil is the largest organic carbon (C) pool in terrestrial ecosystems, and thus even a small variation in soil C stock can significantly change atmospheric CO_2 concentration (Batjes, 1996; Kirschbaum, 2006). The increase in CO_2 can cause a series of global climate and ecosystem changes, including global warming (Hausfather et al., 2022) and plant

Abbreviations: aSOC, annually cycling soil organic carbon; C, carbon; DOC, dissolved organic carbon; dSOC, decadally cycling soil organic carbon; GG, soil obtained from Guigang after 55 years of C_3-C_4 vegetation switch; HA, soil obtained from Harbin after 23 years of C_3-C_4 vegetation switch; MBC, microbial biomass carbon; mSOC, millennially cycling carbon; MTT, microbial turnover time; RCT, relative change in turnover rate; SOC, soil organic carbon.

photosynthesis increases (Keenan et al., 2021; Kumar et al., 2021). Most studies presume that climate warming will accelerate soil organic carbon (SOC) mineralization and increase CO_2 efflux and thus further exacerbate climate warming, forming positive feedback (Melillo et al., 2002; Giardina et al., 2014). However, the intensity of this feedback may largely depend on the response of soil C pools with different turnover rates to warming.

According to the turnover rate, the soil C stocks can be conveniently divided into annually cycling carbon (aSOC), decadally cycling carbon (dSOC), and millennially cycling carbon components (mSOC) (Davidson and Janssens, 2006). The aSOC is relatively labile and has a much small size (only 0%– 5%). The mSOC would be beyond our concerns with the turnover time of a few centuries and much stronger stability (Dungait et al., 2012). The dSOC with turnover times of 10–100 years is the main component of SOC stocks (60%– 85%), and its response to global change will significantly alter the global C cycle (Jones et al., 2005). Therefore, it is crucial to better understand the response of dSOC to warming (Conant et al., 2011).

The response of soil C turnover to warming might depend on the chemical recalcitrance and physical accessibility of microbial substrates, and the change of soil microbial community activity/ composition and extracellular enzymes (Schimel and Schaeffer, 2012; Xu et al., 2018). Relevant observations have shown that 14 years-warming caused shifts in soil microbial community activity/composition and thus accelerated the turnover of labile, but not recalcitrant organic C in a tallgrass prairie soil (Stuble et al., 2019). Microbial community influences on SOC turnover in mineral soils are based on physical access to the occluded or sorbed substrates, and how organisms allocate the C they take up (Xu et al., 2018). Soil C pools containing less labile material have a longer turnover time with higher activation energy, and thus are more temperature-sensitive as projected by a three-pool model (Knorr et al., 2005). However, the underlying mechanisms driving this process are still unclear.

There are two main methods to assess the response of soil C pools to climate warming. Firstly, based on soil respiration rates from laboratory incubation and modeling (Paul et al., 2001; Paterson et al., 2009; Jagadamma et al., 2014; Jiang et al., 2018). Secondly, according to ¹³C isotopic tracer (Martin et al., 1990; Roscoe et al., 2001; Blagodatskaya et al., 2011) or radiocarbon (¹⁴C) dating measurement and modeling (O'Brien et al., 2013; Han et al., 2017; Hall et al., 2018).

In this study, we determined the effect of warming on SOC decomposition *via* the assumed pathway of SOC \rightarrow dissolved organic carbon (DOC) \rightarrow microbial biomass carbon (MBC) \rightarrow CO₂ by using the natural ¹³C isotopic tracing method. The relative change in turnover rate (RCT) of dSOC increased while aSOC decreased in DOC, MBC and CO₂ were assessed in a 1-year incubation experiment using two C₃-C₄ vegetation switch soils at 20°C and 30°C. In this study, we hypothesized that

1) warming increased the contribution of dSOC to DOC, MBC and CO₂; and 2) warming increased the RCT in MBC and CO₂.

Materials and methods

Soil used

Two C₃-C₄ vegetation switch soils were sampled from the plow layer (0–20 cm). One soil was obtained from the experimental station of Heilongjiang Academy of Agricultural Sciences, Harbin, in the northeast of China (HA soil), where C₄-maize ($\delta^{13}C = -13.9\%$) was planted for 23 years after mixed C₃ grass causing a shift in the $\delta^{13}C$ of SOC from -25.6% to -20.4% in HA soil [C_{org} = 17.0 g kg⁻¹; N_{total} = 1.4 g kg⁻¹; pH (CaCl₂) = 6.7]. The other soil was obtained from the agricultural region of Guigang in southwest China (GG soil), where C₄- sugarcane ($\delta^{13}C = -13.0\%$) was grown for 55 years on a C₃ paddy field shifting the $\delta^{13}C$ of SOC from -27.9% to -15.4% in GG soil [C_{org} = 22.6 g kg⁻¹; N_{total} = 2.0 g kg⁻¹; pH (CaCl₂) = 6.9]. These differences in $\delta^{13}C$ were used to distinguish dSOC (C₃ signal) and aSOC (C₄ signal).

Experimental design and soil incubation

The 1-year laboratory incubation experiment on air-dried, root-free soils was executed. The procedures in detail are given in (Lin et al., 2015). Specifically, each soil was screened by 2 mm, mixed evenly, air-dried in the field, and brought back to the laboratory. The plant roots and visible gravel were carefully removed before incubation. 300 g soil was put into a polypropylene column with a diameter of 5 cm and a height of 25 cm. The bottom of the column was plugged with a silicone plug with a hose for ventilation, and the top was covered with a parafilm film with a small hole for water retention and ventilation. Each column was placed in an incubator with an accuracy of ±0.2°C (SHELLAB LI20-2, United States) at 20°C and 30°C. Before the experiment, soil moisture was adjusted to 60% of the maximum soil moisture holding capacity (WHC) by adding deionized water. Soil moisture was kept constant by weighing during the 360-day incubation period. To avoid anaerobic conditions, each column was vented for 1 h each day with CO₂-free air.

Soil respiration and δ^{13} C-CO₂

An improved continuous air-flow CO_2 trapping system was used for soil respiration rate and $\delta^{13}C$ - CO_2 measurement (Virginia, 1993; Lin et al., 2015). Soil respiration and $\delta^{13}C$ - CO_2 were measured at 14, 45, 60, 120, 180, 240, 320, and 360 d. Soil respiration was measured by using an infrared CO₂ analyzer (LiCOR 6262, Lincoln, NB, United Stat) coupled with a digital mass flow meter (GFM17, Aalborg Instruments and Control Inc., New York, United States). The δ^{13} C-CO₂ was measured by analyzing NaOH solution by Cavity Ring-Down Spectroscopy (CRDS) with Automate Module (Picarro G2131-i Analyzer, United States) after CO₂ trapping. Blanks without soil were included as a reference to correct handling errors.

DOC, MBC, SOC, and δ^{13} C

The content and $\delta^{13}C$ of DOC and MBC were measured at 14, 45, 60, 120, 180, 240, 320, and 360 d in HA soil and at 14, 45, 320, and 360 d in GG soil, respectively. The content and δ^{13} C of SOC were measured at 14, 320, and 360 d in soil HA and soil GG. DOC from 50 g soil was extracted with 0.5 M K₂SO₄ in a 1:2 ratio. MBC from another 50 g of soil was fumigated by chloroform and then extracted in the same way. The conversion factor of K_c is 0.38 for MBC (Vance et al., 1987). The extracts were determined by a TOC/TN analyzer (Multi N/C 3100, Analytik Jena, Germany). An aliquot of 20 ml K₂SO₄ extract was measured for the δ^{13} C by Picarro iTOC-CRDS analyzer (Picarro Inc., Santa Clara, CA, United States). In brief, inorganic C in the extracts was removed by 5% phosphoric acid at 70°C, and then organic C in the extract was converted into CO2 by 10% Na2S2O8 at 98°C. SOC was analyzed by dry combustion using an Elementar analyzer (Vario ELIII, elementar, Germany). The $\delta^{13}C$ of SOC was determined by WS-CRDS (Picarro G2131-i Analyzer, Picarro Inc., Santa Clara, CA, United States).

Calculations and statistical analysis

In order to calculate the respiration rate of the soil samples, we used the formula (Tian et al., 2014; Lin et al., 2015):

$$R = [(C-C_0) \times v \times 12 \times 24 \times 60 \times 0.001] / (22.4 \times W)$$
(1)

where R is soil CO₂ efflux (μ g CO₂-C g⁻¹ dry soil day⁻¹), C is the recorded CO₂ concentration (μ mol CO₂ mol⁻¹) in the sample jar, C₀ is the recorded CO₂ concentration in the blank jar, v is the recorded CO₂ flow rate by digital mass flow meter (ml min⁻¹), 22.4 is the molar volume of gas under standard conditions (L/mol), and *W* is gram dry weight of the soil sample.

The portion (*F*) of aSOC (maize or sugar cane-derived C) in DOC, MBC, SOC, and CO_2 was estimated by the following equation (Amelung et al., 2008):

$$F = \left(\delta^{13}C_{t} - \delta^{13}C_{3}\right) / \left(\delta^{13}C_{4} - \delta^{13}C_{3}\right)$$
(2)

where $\delta^{13}C_t$ is the $\delta^{13}C$ value of the C pools (SOC, DOC, MBC) and CO₂-C under maize or sugar cane; $\delta^{13}C_3$ is the $\delta^{13}C$ value of SOC in reference soil with continuous C₃ vegetation (Lin et al., 2015). The $\delta^{13}C$ of DOC, MBC and CO₂-C in reference soil were calculated according to the δ^{13} C shift between SOC and the C pools (Blagodatskaya et al., 2011). The $\delta^{13}C_4$ was calculated based on the δ^{13} C value of maize or sugar cane (mean of leaves, stems and roots) and corrected by subtracting the difference between δ^{13} C of SOC in C₃ reference soil and δ^{13} C of corresponding C₃ plant (i.e., rice, wheat or fescue) by assuming similar isotopic fractionation from C₃ and C₄ plants in humification processes (Schneckenberger and Kuzyakov, 2007).

$$MTT = MBC \times (1-Y) / [(R_s - MBC \times R_m) \times Y]$$
(3)

where R_s is soil respiration rate; MBC is microbial biomass C; Y (microbial substrate utilization efficiency) is 0.45; R_m (soil microbial maintenance respiration rate) is 0.08% of the biomass day⁻¹.

Based on the ¹³C shift, the relative change in the turnover rate (RCT) of dSOC increased while aSOC decreased in DOC, MBC and CO₂ was calculated as follows (Blagodatskaya et al., 2011):

$$RCT = [C_3 - C_{\text{final}}/C_3 - C_{\text{inital}}]/[C_4 - C_{\text{final}}/C_4 - C_{\text{inital}}] \quad (4)$$

where C_3 -C is C_3 -derived C in DOC, MBC or CO₂; C_4 -C is C_4 -derived C in DOC, MBC or CO₂. "Final" represents the stage of the last 45 d during 1-year incubation. "Initial" represents the stage of the first 45d from the beginning of 1-year incubation.

Statistical analyses for all data were performed using SPSS Statistics 20. The Fischer LSD test was used for mean comparisons at p<0.05. Curve fitting was performed using SigmaPlot12.5.

Results

Dynamics of δ^{13} C in CO₂-C, MBC and DOC

The $\delta^{13}C_{CO2}$ continuously depleted with time prolonged and warming, suggesting the C source for microbial respiration increasingly transformed from aSOC to dSOC (Figure 1). The $\delta^{13}C_{MBC}$ firstly increased at the initial stage, and then continuously decreased and was stable at the final stage for both soils at 20°C and 30°C, indicating that a relative contribution switched from aSOC to dSOC for microbial assimilation with the incubation time prolonged. On the contrary, the $\delta^{13}C_{DOC}$ and $\delta^{13}C_{SOC}$ were almost constant throughout the whole incubation and warming, indicating an equal contribution of dSOC and aSOC to DOC.

Contribution of dSOC to CO₂-C, MBC and DOC under warming

At the initial stage (first 45 d) of the incubation, warming increased the C_3/C_{total} by 3% (soil HA) and 7% (soil GG) in MBC, and 9% (soil HA) and 12% (soil GG) in CO₂, while had a



1%–3% increase on C_3/C_{total} in DOC. Furthermore, warming increased the C_3/C_{total} by 21% (soil HA) and 8% (soil GG) in MBC, and 38% (soil HA) and 15% (soil GG) in CO₂, while having a slight increase in C_3/C_{total} in DOC by 2%–3% at the final stage of the incubation (Table 1).

Relative change in turnover rate

Relative change in turnover rate (RCT) in MBC and CO_2 significantly increased with temperature increasing for both soils. However, the RCT in DOC was not significantly different between 20°C and 30°C in soil HA and GG, respectively (Figure 2).

$\delta^{13}C$ shift in the direction of SOC ${\rightarrow}$ DOC ${\rightarrow}$ MBC ${\rightarrow}$ CO_2

Warming simultaneously depleted the δ^{13} C of SOC \rightarrow DOC and MBC \rightarrow CO₂ for soil HA and GG at the initial and final stages (Figure 3). However, warming enriched the δ^{13} C of DOC \rightarrow MBC at the initial stage, while depleting the δ^{13} C of DOC \rightarrow MBC at the final stage for soil HA and GG. The change of the δ^{13} C in DOC \rightarrow MBC further verified that the microbial substrate source transforms from aSOC to dSOC with warming and incubation time.

Discussion

Microbial substrates gradually switched from aSOC to dSOC with warming and prolonged time. Under a sufficient supply of

available substrates, aSOC-derived substrates were immediately preferentially utilized and decomposed by microorganisms metabolically for CO₂ release (Esperschütz et al., 2009; Vain et al., 2021). Under the warming, aSOC was further utilized by microorganisms for soil respiration and microbial assimilation. The δ^{13} C was different in soil C pools and their metabolites (Figure 1). The δ^{13} C pathway of DOC \rightarrow MBC was prolonged, and the absolute δ^{13} C values were enriched by 1.5%–2.6‰ across soil HA and soil GG after warming at the initial stage (left scheme on Figure 3), which further verified that microorganisms selectively utilize more available aSOC that mainly originated from C4-C, i.e., recent C from C₃-C₄ vegetation switch, such as root exudate fractions from DOC at the initial warming stage. On the contrary, compared with the initial stage, the δ^{13} C pathway of DOC \rightarrow MBC shortened with warming and incubation time at the final stage, and the absolute values of δ^{13} C were depleted by 0.3%–0.8‰ across the two soils (right scheme Figure 3). This indicated a decreased microbial uptake of aSOC from DOC, so that more dSOC was assigned to microbial growth and respiration, which enhanced the contribution of dSOC to MBC and CO2 with incubation prolonged and warming (Table 1).

The RCT is an indicator of the relative change in the turnover rate of dSOC (C3-C) increased when aSOC (C4-C) decreased, which is more indicative here as the relative contribution of dSOC in MBC or CO₂ increased while those of aSOC decreased during the 360-d incubation (Blagodatskaya et al., 2011). The RCT in MBC and CO2 were much higher at the higher temperature in Figure 2, which confirmed that warming accelerates the relative change in the turnover rate of dSOCderived C in MBC and CO₂. Nutrient availability impacts the response of SOC pools to warming by altering substrate stabilization, microbial community composition and extracellular enzyme activity (Doetterl et al., 2018). SOC

C ₃ -C ₄ soil		HA soil						GG soil					
C Source	T (°C)	DOC		MBC		CO ₂		DOC		МВС		CO ₂	
		Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final
total	20	123.2 ^{Ab} ±9.9	62.2 ^{Bb} ±1.8	170.0 ^{Ab} ±5.2	154.1 ^{Bb} ±3.4	8.5 ^{Ab} ±0.2	6.5 ^{Bb} ±0.3	85.0 ^{Aa} ±3.1	55.4 ^{Ba} ±0.6	298.9 ^{Aa} ±8.5	267.0 ^{Ba} ±0.7	21.6 ^{Aa} ±0.6	12.3 ^{Ba} ±0.8
	30	123.8 ^{Ac} ±8.0	62.1 ^{Bb} ±2.3	170.4 ^{Ab} ±5.4	120.6 ^{Bc} ±4.7	11.7 ^{Aa} ±0.6	9.4 ^{Ba} ±0.3	82.6 ^{Aa} ±0.8	54.1 ^{Ba} ±0.7	279.9 ^{Aa} ±3.4	249.5 ^{Bb} ±1.9	26.3 ^{Aa} ±0.4	14.6 ^{Bb} ±0.2
C ₄	20	6.2 ^{Aa} ±0.3	4.1 ^{Bb} ±0.1	46.1 ^{Ab} ±4.7	45.1 ^{Bb} ±0.6	5.2 ^{Ab} ±0.1	3.6 ^{Bb} ±0.2	10.4 ^{Aa} ±0.4	5.6 ^{Ba} ±0.07	90.5 ^{Aa} ±0.8	53.7 ^{Ba} ±0.4	18.1 ^{Aa} ±0.8	6.6 ^{Ba} ±0.4
	30	4.6 ^{Aa} ±0.2	3.0 ^{Bb} ±0.1	51.3 ^{Aa} ±3.3	10.1 ^{Bb} ±3.5	6.1 ^{Aa} ±0.2	1.6 ^{Bab} ±0.1	7.7 ^{Ab} ±0.8	4.0 ^{Bb} ±0.2	104.5 ^{Ab} ±4.9	30.4 ^{Bb} ±3.5	18.8 ^{Aa} ±0.3	5.6 ^{Bb} ±0.1
C ₃	20	116.9 ^{Aa} ±3.3	58.1 ^{Bb} ±2.0	124.0 ^{Bb} ±5.4	109.1 ^{Ab} ±1.3	3.3 ^{Ab} ±0.1	2.9 ^{Bb} ±0.1	74.6 ^{Aa} ±3.4	49.9 ^{Aa} ±0.6	208.5 ^{Aa} ±8.9	213.3 ^{Aa} ±1.1	3.5 ^{Aa} ±0.4	5.7 ^{Ba} ±0.4
	30	119.2 ^{Aa} ±0.9	59.1 ^{Bb} ±0.5	119.1 ^{Bc} ±4.3	110.6 ^{Ac} ±6.1	5.6 ^{Aa} ±0.1	7.7 ^{Ba} ±0.1	74.9 ^{Aa} ±1.2	50.2 ^{Aa} ±0.6	175.5 ^{Ab} ±6.7	219.1 ^{Ba} ±2.6	7.5 ^{Ab} ±0.2	9.1 ^{Bb} ±0.1
C_4/C_{total}	20	0.05	0.07	0.27	0.29	0.62	0.55	0.12	0.10	0.30	0.20	0.83	0.53
	30	0.04	0.05	0.30	0.08	0.53	0.17	0.09	0.07	0.37	0.12	0.71	0.38
C ₃ /C _{total}	20	0.95	0.93	0.73	0.71	0.38	0.45	0.88	0.90	0.70	0.80	0.17	0.47
	30	0.96	0.95	0.70	0.92	0.47	0.83	0.91	0.93	0.63	0.88	0.29	0.62
C ₄ (final/initial stage)	20	1.52		1.10		0.90		0.82		0.67		0.65	
	30	2.28		0.28		0.33		0.81		0.33		0.54	
C ₃ (final/initial stage)	20	0.98		0.97		1.16		1.03		1.15		2.39	
	30	0.99		1.32		1.74		1.02		1.40		2.16	





FIGURE 2

RCT variation after 1-year incubation at 20 C and 30 C. RCT is an indicator as the relative change of contribution of C_3 -C in DOC, MBC, and CO₂-C increased while that of C_4 -C decreased during the incubation. Different lowercase letters denote significant differences at p < 0.05 level between 20°C and 30 C.



turnover mostly involves several steps with distinct inherent kinetics, such as aggregate disruption and then exoenzymes breaking up the polymers (Liang and Balser, 2011; Poeplau et al., 2017). Microbial biomass is a small size and relatively labile C pool, and thus it turnovers much quicker relative to SOC. Microbial growth may primarily utilize the dead cells and dSOC under a shift of C substrate types with incubation time. Warming might intensify the decomposition of the dSOC by deactivating

aggregate-binding (Poeplau et al., 2017). Once dSOC loses the physi-chemical protection of soil aggregates, it will be exposed to microorganisms. Thus, microorganisms can quickly access dSOC and further improve the turnover of SOC at the final stage of the incubation. A meta-analysis showed that C-degradation-related enzyme activities differentially respond to warming. Ligninase activity and turnover of recalcitrant C pools were gradually enhanced with experiment duration and warming (Chen



et al., 2018). Another relevant study found that a 14-year warming-induced change in the shift of soil microbial community activity and composition accelerated the turnover of labile, but not recalcitrant C pools (Stuble et al., 2019). Similarly, warming-induced losses of unprotected SOC were detected from 4 to 9 years of whole-ecosystem warming experiments in a grassland (Phillips et al., 2016).

The average microbial turnover time (MTT) was estimated according to the amount of CO2-C respired compared to the amount of MBC by assuming a steady state at the final stage of incubation (Eq. 3). It was observed that warming accelerated the turnover of microbial biomass by 1.6-2.6 and 1.5-2.0 times in dSOC- and aSOC-derived MBC, respectively (Figure 4). The MTT was estimated as 17.7-47.2 d and 6.6-15.4 d in dSOC- and aSOC-derived MBC across two soils and two temperatures in this study (Figure 4), which is lower than that of 64.5 d in dSOC and 20.7 d in aSOC reported in Blagodatskaya et al. (2011). Obviously, the sensitivity of dSOC- and aSOC-derived MBC turnover to warming is inconsistent. Furthermore, Li et al. (2019) found that warming increases microbial biomass turnover using a probabilistic inversion approach by integrating a microbialenzyme model with two decades of soil warming measurement. However, the difference in temperature sensitivity of microbial turnover in soil C pools with different turnover rates (such as aSOC and dSOC) is not considered in the model predictions. It is crucial to accurately evaluate the prediction of soil C budget caused by warming. Thus, it should be focused on in the following research.

Conclusion

Based on a natural ¹³C isotopic tracer, the effect of warming on RCT of dSOC in DOC, MBC and CO_2 was investigated by incubating two C_3 - C_4 vegetation switch soils

for 1 year. Warming increased the contribution of dSOC to total SOC by 8%–21% in MBC, and 15%–38% in CO₂, while only 2%–3% in DOC. The RCT in MBC and CO₂ increased by 5.3- and 4.1-fold due to warming, respectively, but had no significant variation in DOC, indicating that soil microbes may be an important engine to accelerate dSOC-derived CO₂ emission in a warming world. The following research should focus on microbial regulation in the dSOC transformation process and temperature sensitivity of soil C pools with distinct turnover rates in MBC and CO₂ for correctly projecting the feedback between climate warming and soil C storage.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

QN and DL designed the experiment; CX and DL performed the experiments; DL and WZ analyzed the data and wrote the manuscript; All authors revised the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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