REGULAR ARTICLE

Terrestrial C:N stoichiometry in response to elevated CO_2 and N addition: a synthesis of two meta-analyses

Yuanhe Yang · Yiqi Luo · Meng Lu ·
Christina Schädel · Wenxuan Han

Abstract Both elevated atmospheric carbon dioxide (CO_2) and nitrogen (N) deposition may induce changes in C:N ratios in plant tissues and mineral soil. However, the potential mechanisms driving the stoichiometric shifts remain elusive. In this study, we examined the responses of C:N ratios in both plant tissues and mineral soil to elevated CO_2 and N deposition using data extracted from 140 peer-reviewed publications. Our results indicated that C:N ratios in both plant tissues and mineral soil exhibited consistent increases under elevated CO_2 regimes whereas decreases in C:N ratios were observed in response to experimental N addition. Moreover, soil C:N ratio was less sensitive than plant C:N ratio to both global change scenarios. Our results also showed that the responses of stoichiometric ratios were highly variable among different studies. The changes in C:N ratio did not exhibit strong correlations with C dynamics but were negatively associated with corresponding changes in N content. These results suggest that N dynamics drive stoichiometric shifts in both plant tissues and mineral soil under both elevated CO_2 and N deposition scenarios.

Keywords Carbon:nitrogen ratio · Global change · Mineral soil · Nitrogen deposition · Plant tissues · Stoichiometric shift · Terrestrial ecosystems

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Y. Yang (✉) · Y. Luo · C. Schädel
Department of Botany and Microbiology,
University of Oklahoma,
Norman, OK 73019, USA
e-mail: yhyang@ou.edu

M. Lu
Coastal Ecosystems Research Station of Yangtze
River Estuary, Ministry of Education Key Laboratory
for Biodiversity Science and Ecological Engineering,
The Institute of Biodiversity Science, Fudan University,
220 Handan Road,
Shanghai 200433, China

M. Lu
Department of Environmental Science and Engineering,
Fudan University,
220 Handan Road,
Shanghai 200433, China

W. Han
College of Resources and Environmental Sciences,
China Agricultural University,
Beijing 100094, China

Introduction

Human activities have induced significant environmental changes, such as rising atmospheric carbon dioxide (CO_2) and enhanced nitrogen (N) deposition (Forster et al. 2007). These environmental changes have affected global biogeochemical cycles, particularly C (Heimann and Reichstein 2008) and N (Gruber and Galloway 2008) cycling in natural ecosystems. The altered ecosystem C and N cycles may lead to stoichiometric shifts in C:N ratios in both plant tissues and mineral soil (Sterner and Elser 2002; Novotny et al. 2007). Conversely, the stoichiometric flexibility in elemental ratios may influence biogeochemical cycles in natural ecosystems through their effects on ecosystem production and decomposition processes (Luo et al. 2004). Thus, our knowledge of the stoichiometric responses to global environmental changes is crucial for understanding future biogeochemical cycles in terrestrial ecosystems (Sterner et al. 2007; Elser et al. 2009a, b, 2010).

It has been suggested that increased CO_2 and N supply might drive plant stoichiometry in opposite directions (McGuire et al. 1995; Esmeijer-Liu et al. 2009). Elevated CO_2 usually leads to an increase in plant C:N ratio (McGuire et al. 1995; Gifford et al. 2000; Norby et al. 2001; Novotny et al. 2007; Esmeijer-Liu et al. 2009), while atmospheric N deposition frequently results in a decrease in plant C:N ratio (Wedin and Tilman 1996; Novotny et al. 2007; Esmeijer-Liu et al. 2009). However, our current understanding is mainly derived from plants and little information is available for mineral soil. Moreover, the effects of N deposition on C:N ratios in both plant tissues and mineral soil are not well quantified in comparison with elevated CO_2. In addition, the potential factors driving the responses of stoichiometric ratios to global environmental changes have not been well documented. This study was designed to examine the responses of C:N ratios in both plant tissues and mineral soil to elevated CO_2 and experimental N addition, based on two databases compiled by Luo et al. (2006a) and Lu et al. (2010a, b). Specifically, this study aims at (1) quantifying changes in C:N ratios in both plant tissues and mineral soil under elevated CO_2 and experimental N addition, and (2) examining potential factors that drive C:N ratio dynamics in response to both global change scenarios.

Materials and methods

Data sources

Data used in this study were derived from two databases compiled by Luo et al. (2006a) and Lu et al. (2010a, b), respectively (Supplemental Appendix S1, S2). The database by Luo et al. (2006a) documented C and N contents under ambient and elevated CO_2 regimes, which were extracted from 104 peer-reviewed publications. The database consisted of two parts: plant-based and area-based records. The plant-based data were mostly obtained from growth chamber studies, whereas the area-based data were mainly from free-air CO_2 enrichment and open-top chamber studies (Luo et al. 2006a). In this study, only the area-based records were used due to the lack of data on plant C concentration and on soil C and N information in the plant-based dataset. The database by Lu et al. (2010a, b) included detailed records of C and N contents under ambient and elevated N scenarios, which were synthesized from 206 peer-reviewed publications. The database included 33 variables about C and N pools, fluxes, and other related parameters in response to experimental N addition (Lu et al. 2010a, b). In this synthesis, we used data of C and N contents to explore the changes in C:N ratios in shoot, root, and mineral soil with the external N input.
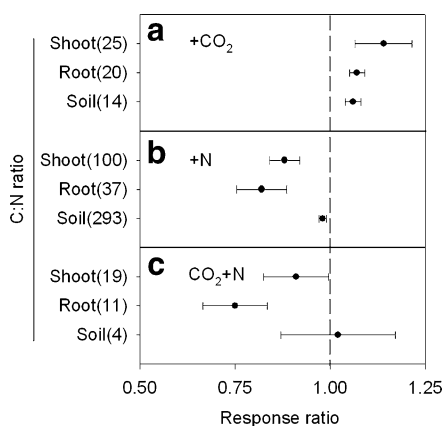
Data analyses

We calculated the response ratio (RR) to reflect the effects of elevated CO_2 and N addition on C:N ratios in various ecosystem components (i.e. shoot, root and mineral soil). RR, the ratio of the mean value of the chosen variable in the treatment group ($\overline{Xt}$, C:N ratio under experimental treatment) to that in the control group ($\overline{Xc}$, C:N ratio under control condition), is an index of the effect of the experimental treatment on the target variable (Hedges et al. 1999). The treatment effect of elevated CO_2 and/or N addition was considered to be significant if the 95% confidence interval of RR did not overlap with 1.0 (Hedges et al. 1999). We then investigated the relationships between the RR of C content and the RR of N content under both global change scenarios. We further examined the relationships of the RR of C:N ratio with the RR of C and N content under both global change scenarios. All statistical analyses were performed using the

software package R 2.11.0 (R Development Core Team 2010).

Results

Elevated CO_2 led to significant increases in C:N ratios in various ecosystem components ($P<0.05$) (Fig. 1a). Specifically, C:N ratios increased from 66.2 to 71.3 for shoot, from 43.8 to 46.6 for root, and from 22.1 to 22.7 for mineral soil under elevated CO_2 conditions (Supplemental Table S1). However, the responses of stoichiometric ratios revealed a wide range of variations, ranging from a 25% decrease to a 66% increase for shoot, −2%~30% for root, and −25%~18% for mineral soil. Overall, C:N ratio exhibited an average increase of 13.8% for shoot, 6.6% for root, and 4.1% for mineral soil (Supplemental Table S1). In contrast, N addition induced significant decreases in C:N ratios in various ecosystem components (i.e. from 46.1 to 39.9 for shoot, from 50.6 to 39.4 for root, and from 14.9 to 14.5 for mineral soil) (Fig. 1b, Supplemental Table S1). Also, the responses of C:N ratios exhibited large variations among different studies, ranging from a 58% decrease to a 62% increase for shoot, −66%~20% for root, and −69%~55% for mineral soil), with an average decrease of 11.7% for shoot, 18.4% for root, and 2.2% for mineral soil (Supplemental Table S1). In addition, C:N ratios in both shoot and root tissues significantly decreased in response to elevated CO_2+N addition ($P<0.05$), while no significant effects were detected for C:N ratio in mineral soil due to the small sample size ($P=0.67$, Fig. 1c).

The RR of C content was positively correlated with the RR of N content in all ecosystem components under both elevated CO_2 and experimental N addition scenarios ($P<0.05$, Fig. 2). However, the large variability in C:N ratio dynamics in response to both elevated CO_2 and experimental N addition was largely driven by N dynamics (Fig. 3, 4). Specifically, the RR of C:N ratio exhibited weak associations with the RR of C content ($P>0.05$ for all ecosystem components) (Fig. 3a-c-e), whereas there was a negative relationship to the RR of N content under elevated CO_2 ($r^2=0.39$, $P<0.05$ for shoot; $r^2=0.36$, $P<0.05$ for root; $r^2=0.70$, $P<0.05$ for mineral soil) (Fig. 3b-d-f). Similarly, the RR of C:N ratio exhibited significant negative associations with the RR of N content in shoot ($r^2=0.24$, $P<0.05$) (Fig. 4b), root ($r^2=0.50$, $P<0.05$) (Fig. 4d) and mineral soil ($r^2=0.19$, $P<0.05$) (Fig. 4f) under N addition. However, besides that in mineral soil ($r^2=0.20$, $P<0.05$) (Fig. 4e), the RR of C:N ratio did not show any significant correlations with the RR of C content in plant tissues under experimental N addition ($P>0.05$) (Fig. 4a, c).
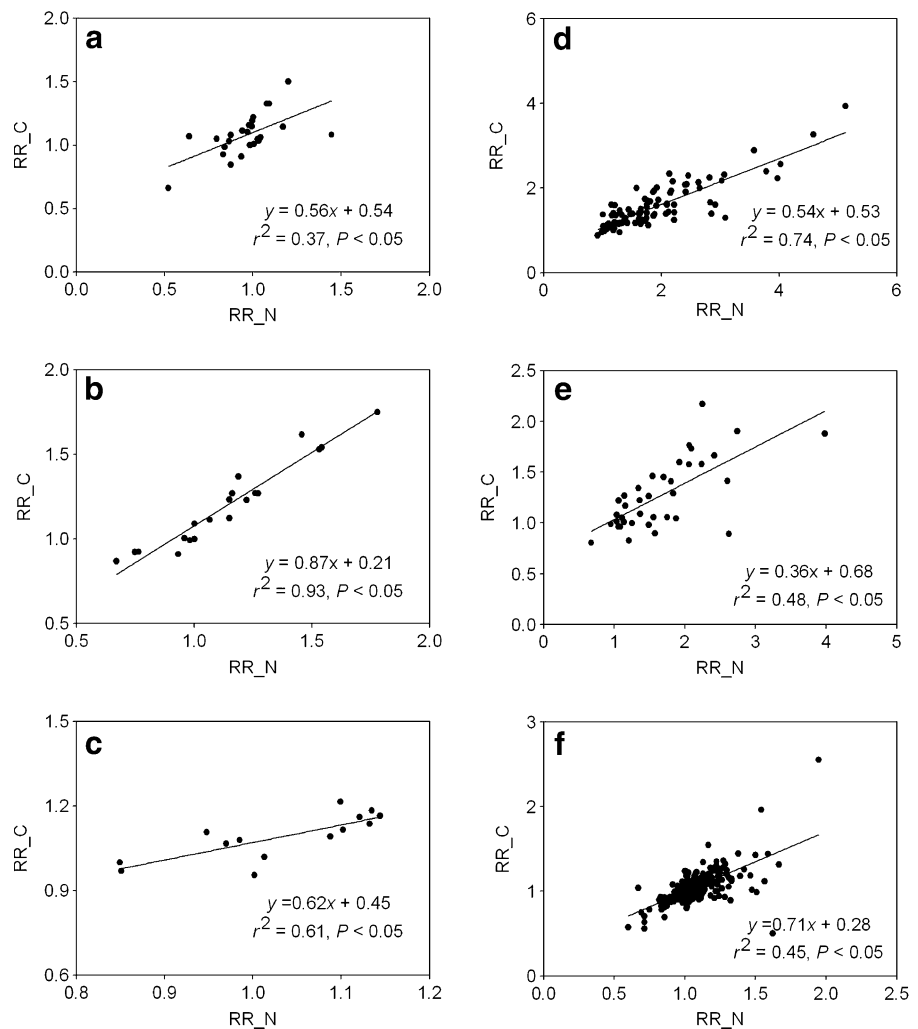
Discussion

Shifted C:N ratio due to elevated CO_2 and N addition

Plant C:N ratios increased under elevated CO_2 regimes. The increase of plant C:N ratio may be due to a dilution of the N concentration by the accumulation of non-structural carbohydrates (Poorter et al. 1997; Güsewell 2004), and the relative increase in the synthesis of C-based secondary metabolic products that are low in N concentration, such as lignin (Gifford et al. 2000). The increased plant C:N ratio may also be indirectly driven by the shifts of biomass partitioning towards tissues owning a relatively low N concentration (e.g. wood) (Gifford et al. 2000; Elser et al. 2010), and the metabolic down-regulation of enzymes involved in photosynthesis under the elevated CO_2 scenario (Gifford et al. 2000; Elser et al. 2010).

By contrast, experimental N addition induced substantial decreases in plant C:N ratios. The decreases in plant C:N ratios may be due to reduced N use efficiencies (i.e. plant production per unit N) under

Fig. 1 Effects of elevated CO_2 (**a**), experimental N addition (**b**), and elevated CO_2+N addition (**c**) on C:N ratios in shoot, root and mineral soil. Dots and *error bars* show the overall mean response ratio with a 95% confidence interval. The numbers in parentheses are sample sizes involved in each variable

Fig. 2 Relationships between the response ratio (*RR*) of C content and the *RR* of N content under elevated CO_2 (**a**–**c**) and experimental N addition (**d**–**f**). **a**, **d**: shoot, **b**, **e**: root, and **c**, **f**: soil

Plot a: $y = 0.56x + 0.54$, $r^2 = 0.37$, $P < 0.05$

Plot d: $y = 0.54x + 0.53$, $r^2 = 0.74$, $P < 0.05$

Plot b: $y = 0.87x + 0.21$, $r^2 = 0.93$, $P < 0.05$

Plot e: $y = 0.36x + 0.68$, $r^2 = 0.48$, $P < 0.05$

Plot c: $y = 0.62x + 0.45$, $r^2 = 0.61$, $P < 0.05$

Plot f: $y = 0.71x + 0.28$, $r^2 = 0.45$, $P < 0.05$

higher N levels (Vitousek and Howarth 1991; Chapin et al. 2002). It is well established that external N input usually stimulates plant growth (Lebauer and Treseder 2008), while plant N use efficiency declines with increases in soil N availability (Yuan et al. 2006). The decreased N use efficiency in plants could thus induce the smaller C:N ratio under higher N scenario. The decreases in plant C:N ratio may also be ascribed to the limiting effects of other environmental factors, such as soil phosphorous availability, which may constrain the responses of vegetation growth to the external N input (Vitousek and Howarth 1991; Elser et al. 2007; Reich et al. 2009; Vitousek et al. 2010). Even more, it has been suggested that phosphorous limitation may be enhanced under the atmospheric N deposition scenario (Johnson et al. 1999; Thayer et al. 2008; Elser et al. 2009a, b). As a consequence, the limitation of other nutrients may

constrain C accumulation in terrestrial ecosystems under higher N scenarios and then lead to the stoichiometric shifts in plant tissues.

The C:N ratio in mineral soil increased under elevated CO_2 regimes but decreased in response to experimental N addition. The responses of soil C:N ratio may be largely driven by the corresponding responses of plant C:N ratio since plant detritus is a major C input into mineral soil (Cleveland and Liptzin 2007; Yang et al. 2010a, b). It has been observed that the stoichiometric ratio in mineral soil exhibited close correlations with that in plant tissues (Elser et al. 2010). Thus, the increases in plant C:N ratio under elevated CO_2 regimes may ultimately result in the increases in soil C:N ratio, and the decreases in plant C:N ratio under N addition scenarios may also eventually lead to the decreases in soil C:N ratio. Interestingly, the relative changes in soil
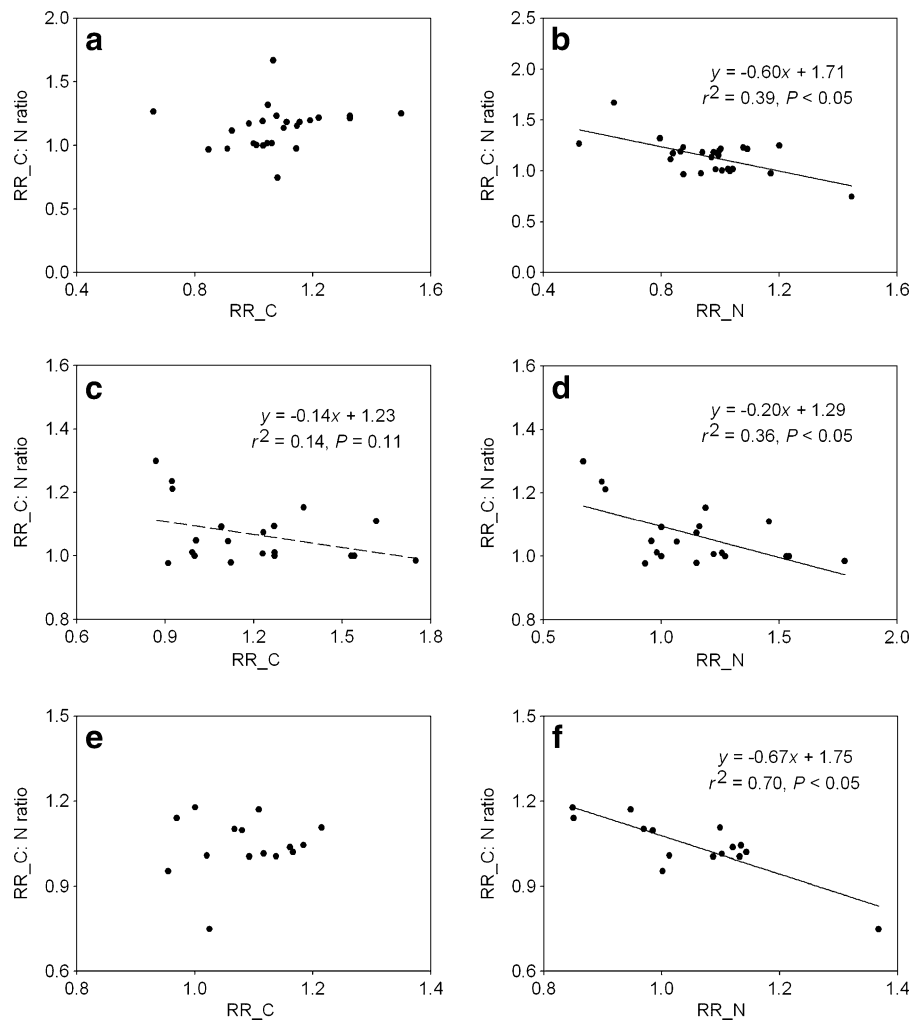
C:N ratios were smaller than plant C:N ratios under both global change scenarios, suggesting that C:N ratios in mineral soils are less sensitive to global environmental changes than are C:N ratios in plants. These differences may be due to the effects of nutrient absorption on C:N ratio in organic matter during litterfall (McGroddy et al. 2004) and the effects of microbial regulation on C:N ratio in organic matter during litter decomposition (Cleveland and Liptzin 2007; Manzoni et al. 2010). Such a pattern may also be due to short experimental duration involved in various individual studies. Plant C:N ratio could be shortly altered under both elevated CO_2 and N addition scenarios but not soil C:N ratio since it takes more time to return litterfall to mineral soil. In addition, the smaller flexibility in soil C:N ratio than plant C:N ratio may be due to the narrow range of C:N ratio in mineral soil compared with that in plant tissues. Nevertheless, future experiments are required to carefully examine the potential mechanisms responsible for such a pattern.

N dynamics drive stoichiometric shifts in response to global change

The changes in C:N ratios exhibited stronger correlations with N than C dynamics in most ecosystem components, indicating that C:N ratio dynamics in response to elevated CO_2 and experimental N addition are primarily determined by N changes. This pattern may be derived from the larger variation in plant N concentration than in plant C concentration (Güsewell 2004). Under natural conditions, it is well known that the C concentration per dry weight is almost constant in all parts of plants (He et al. 2006), while the N concentration per biomass varies in the order of magnitude between different plant organs (e.g. leaf vs. stem or fine vs. coarse root) and also varies

Fig. 4 Relationships of the response ratio (*RR*) of C:N ratio with the *RR* of C and N content in various ecosystem components under experimental N addition. **a–b**: shoot, **c–d**: root, and **e–f**: mineral soil
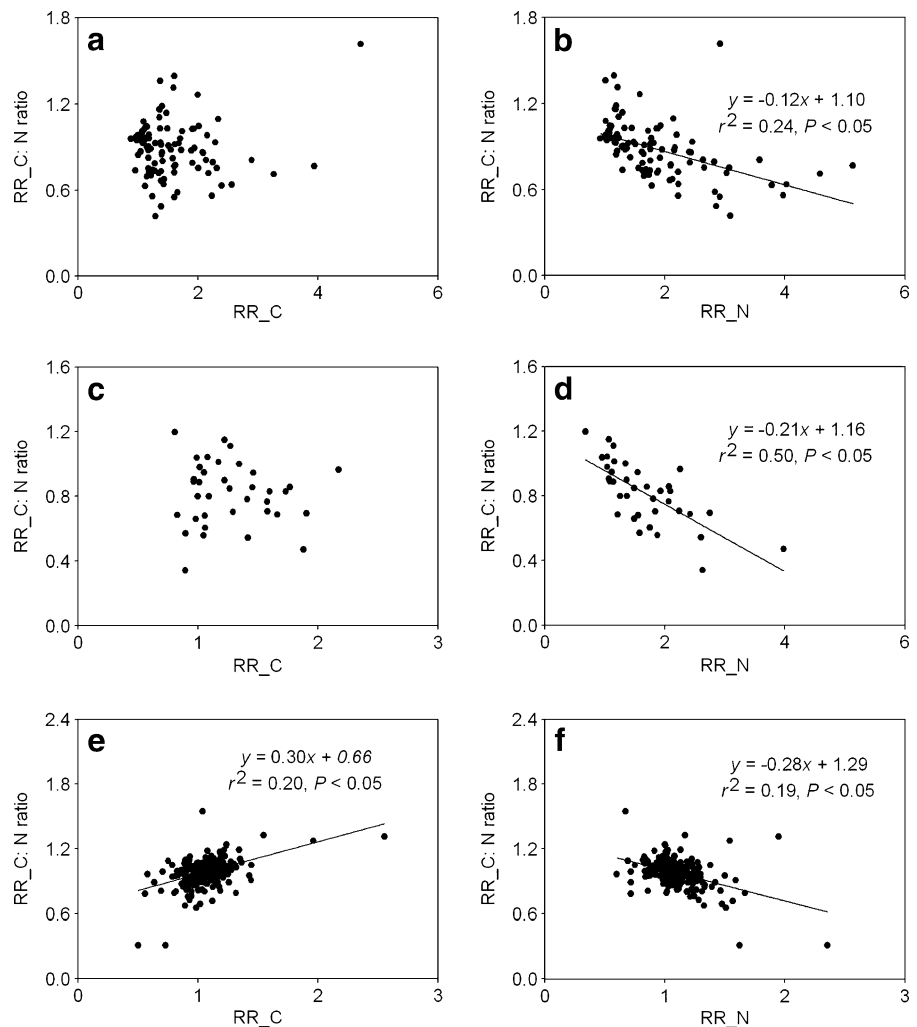
substantially for organs of different plants (Reich and Oleksyn 2004; He et al. 2006). Likewise, it has been frequently observed that plant N concentration is sensitive to both elevated CO_2 (e.g. McGuire et al. 1995; Cotrufo et al. 1998; Güsewell 2004) and experimental N addition (e.g. Reich et al. 2001; Knops et al. 2007). Specifically, plant N concentration was often observed to decrease under elevated CO_2 (e.g. McGuire et al. 1995; Cotrufo et al. 1998; Güsewell 2004) while increasing under experimental N addition (e.g. Reich et al. 2001; Knops et al. 2007). In contrast, plant C concentration was frequently reported to be relatively constant under both elevated CO_2 (e.g. Billes et al. 1993; Luo et al. 2006b) and experimental N addition (e.g. Emmett et al. 1995; Luo et al. 2006b; Cui et al. 2010). As a consequence, the stronger responses of N than C concentration in plant tissues could regulate

the stoichiometric balance in plant tissues and mineral soil under both elevated CO_2 and experimental N addition scenarios.

In summary, this study examined the effects of elevated CO_2 and experimental N addition on C:N ratios in both plant tissues and mineral soil. Our results showed that elevated CO_2 led to increases in C:N ratios in both plant tissues and mineral soil, while experimental N addition resulted in decreases in C:N ratios in both plant tissues and mineral soil. The changes in soil C:N ratio were smaller than the corresponding changes in plant C:N ratio in response to both global change scenarios. Our results also indicated that shifts in C:N ratios were largely determined by N dynamics under both global change scenarios. These results suggest that increases in external resource availability could induce the stoichiometric shifts in plant tissues and

mineral soil by altering N content. Conversely, the C:N ratio dynamics induced by both elevated CO_2 and experimental N addition may exert significant effects on global biogeochemical cycles. The increased C:N ratio driven by elevated CO_2 may prevent litter decomposition and thus lead to progressive N limitation on terrestrial C sequestration (Strain and Bazzaz 1983; Luo et al. 2004). The decreased C:N ratio under experimental N addition implies that N deposition may not make a large contribution to additional C sequestration due to the decreased N use efficiency in terrestrial ecosystems. Nevertheless, it should be noted that the C:N ratio dynamics in terrestrial ecosystems will be determined by the balance between the increases driven by elevated CO_2 and the decreases induced by N deposition. The antagonistic effects of elevated CO_2 and N deposition on C:N ratios may mitigate the subsequent effects of stoichiometric shifts on biogeochemical cycles in terrestrial ecosystems.

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