ELEVATED CO$_2$ STIMULATES NET ACCUMULATIONS OF CARBON AND NITROGEN IN LAND ECOSYSTEMS: A META-ANALYSIS

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Abstract. The capability of terrestrial ecosystems to sequester carbon (C) plays a critical role in regulating future climatic change yet depends on nitrogen (N) availability. To predict long-term ecosystem C storage, it is essential to examine whether soil N becomes progressively limiting as C and N are sequestered in long-lived plant biomass and soil organic matter. A critical parameter to indicate the long-term progressive N limitation (PNL) is net change in ecosystem N content in association with C accumulation in plant and soil pools under elevated CO$_2$. We compiled data from 104 published papers that study C and N dynamics at ambient and elevated CO$_2$. The compiled database contains C contents, N contents, and C:N ratio in various plant and soil pools, and root:shoot ratio. Averaged C and N pool sizes in plant and soil all significantly increase at elevated CO$_2$ in comparison to those at ambient CO$_2$, ranging from a 5% increase in shoot N content to a 32% increase in root C content. The C and N contents in litter pools are consistently higher in elevated than ambient CO$_2$ among all the surveyed studies whereas C and N contents in the other pools increase in some studies and decrease in other studies. The high variability in CO$_2$-induced changes in C and N pool sizes results from diverse responses of various C and N processes to elevated CO$_2$. Averaged C:N ratios are higher by 3% in litter and soil pools and 11% in root and shoot pools at elevated relative to ambient CO$_2$. Elevated CO$_2$ slightly increases root:shoot ratio. The net N accumulation in plant and soil pools at least helps prevent complete down-regulation of, and likely supports, long-term CO$_2$ stimulation of C sequestration. The concomitant C and N accumulations in response to rising atmospheric CO$_2$ may reflect intrinsic nature of ecosystem development as revealed before by studies of succession over hundreds to millions of years.

Key words: carbon sequestration; ecosystem development; global change; meta-analysis; nitrogen; stoichiometry.

INTRODUCTION

The CO$_2$ concentration in the atmosphere (C$_a$) has increased by approximately 35% since the industrial revolution and is predicted to reach 700 μmol/mol by the end of this century due to fossil fuel burning and land cover change (Houghton et al. 2001). To eventually stabilize C$_a$ and prevent dangerous interference with the climate system, we have to understand the role of terrestrial ecosystems in sequestering anthropogenic CO$_2$. The Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) predicts that the C$_a$ increase alone could stimulate terrestrial carbon (C) sequestration by 350–980 Gt (1 Gt = 1 × 10^{15} g) C in the 21st Century (Houghton et al. 2001). Sequestering 350–980 Gt C in terrestrial ecosystems requires 7.7–37.5 Gt of nitrogen (N) according to the calculation made by Hungate et al. (2003). The cal-

culation is based on a stoichiochemical relationship (Hessen et al. 2004) that approximately 0.005 g N is required for 1 g C stored in long-lived plant biomass (i.e., wood) and 0.067 g N for 1 g C sequestered in soil organic matter (SOM). Thus, to realistically predict future C sequestration in terrestrial ecosystems, we have to understand how closely C and N processes are coupled in response to rising C$_a$.

The C and N interactions have been extensively examined in natural ecosystems with or without manipulations of environmental factors. In manipulative experiments with elevated CO$_2$ concentrations, for example, scientists have studied numerous N processes, such as tissue nitrogen concentrations (Peterson et al. 1999), litter quality and decomposition (Norby et al. 2001), soil mineralization (Gill et al. 2002, Zak et al. 2003), N fixation (Hungate et al. 2004), N losses in aqueous and gaseous forms (Reich et al. 2001, Moiser et al. 2002), and plant–microbial competition (Hu et al. 2001). Most of the studies have primarily focused on short-term regulation of plant productivity by soil N availability. The productivity-oriented studies are useful for understanding responses of plant growth and biomass production to rising C$_a$. To predict future eco-

system C sequestration, we have to study long-term interactions between C and N cycles in both plant and soil components of ecosystems. Recently, Luo et al. (2004) proposed a conceptual framework of progressive N limitation (PNL) in recognition that the long-term N availability in ecosystems is governed by sequestration of N in long-lived plant biomass and SOM in association of C sequestration in those pools. The key parameters to indicate PNL include C and N accumulations in plant and soil pools, and stoichiometrical flexibility in C:N ratios in various pools.

In the past decades, scores of experiments have been conducted to examine interactions between ecosystem C and N processes under elevated CO_2. Experimental results are highly variable, ranging from substantial net accumulations of C and N in plant soil and pools (Jastrow et al. 2000, Hamilton et al. 2002) to strong N limitation of plant growth (Oren et al. 2001) and no change in N processes (Billings et al. 2002) at elevated CO_2 compared to those at ambient CO_2. Moreover, ecosystem C and N processes vary considerably over time. N fixation at elevated CO_2, for example, is higher than that at ambient CO_2 in the first two years, followed by a decline (Hungate et al. 2004). The inconsistent results among studies and over time impede our understanding of the C–N coupling and hinder the extrapolation of experimental findings to predict long-term C sequestration at the regional and global scales.

The high variability in experimental observations primarily results from intrinsic heterogeneity in C and N processes over time and across ecosystems. The high variability also masks treatment effects of elevated CO_2, which are usually very small relative to the pool sizes themselves (e.g., Schlesinger and Lichter 2001). Hungate et al. (1996) conducted a statistical power analysis for detecting changes in soil C pools in CO_2 experiments. It takes four and nine years before significant increases in soil C contents can be statistically identified if elevated CO_2 increases new C input into soil by 70% and 35%, respectively. If the new C input into soil only increases by 7% in elevated CO_2, CO_2-induced changes in soil C contents could be too small to be statistically detected, even in a very long-term experiment. Thus, it is crucial to employ other methods to increase the statistical power for ecosystem C research.

In this study, we conducted a meta-analysis of data on C and N processes in plant and soil in response to rising C_a to reveal general patterns among different studies across ecosystems. The meta-analysis also has the potential to make the site-specific, temporally variable results useful for regional and global modeling (Norby et al. 2001, Rustad et al. 2001) and increases the statistical power to detect changes in C and N processes under elevated CO_2. The primary focus of this study is on variables that are critical for testing PNL hypothesis. The variables include C and N contents in various plant and soil pools and their stoichiometrial

flexibility. These variables are presumably indicative of long-term dynamics of C and N interactions (Rastetter et al. 1997, Luo et al. 2004), being complementary to studies on short-term C and N dynamics. Our meta-analysis also included root:shoot (R:S) ratio, which has been suggested as a mechanism of plants to take up more nutrients at elevated than ambient CO_2 (Rogers et al. 1996).

METHODS

Data sources

We collected data from 104 published papers in the literature (see Appendix A) that report results from experiments with ambient and elevated CO_2 treatments. All the original data are extracted from figures and tables in the published papers. The constructed database consists of 940 lines of entries, each containing sources of data, experimental facilities, ecosystem types, field sites, exposure times, nitrogen treatments, CO_2 concentrations of treatments, and 18 variables (see Appendix B). Experimental facilities are divided into free-air CO_2 Enrichment (FACE), open-top chamber (OTC), and growth chamber (GC). Studies with plants grown in pots in greenhouses and growth chambers are lumped together into the category of GC. Ecosystem types include forest, grassland, wetland, cropland, and desert. Exposure times are the durations from the start of experiments to the time when data are collected and are in unit of year. Any exposure times that are less than one year are approximated by one year. Regardless of experimental duration, the exposure time is one year for annual crops if plant biomass is analyzed. Nitrogen treatments are only qualitatively divided into low and high. If there are more than two levels of N treatments, the lowest and highest treatments are included into the database. Treatments of other factors (e.g., temperature, O_3, and species compositions) are not explicitly analyzed, but data at all the treatments are included in the meta-analysis.

The 18 variables collected from papers describe biomass in aboveground shoot, belowground root, and whole plant; C pools in shoot, root, whole plant, litter, and soil; N pools in shoot, root, whole plant, litter, and soil; ratios of C and N in shoot, root, litter, and soil pools; and root:shoot ratio. For each of the 18 variables, we extracted means, standard errors, and sample sizes. The database is divided into area-based and plant-based data. The plant-based data are mostly from GC studies with units of C and N per plant while the area-based data are mostly from FACE and OTC studies. Data of C and N pools from the FACE and OTC studies are expressed in, or converted to if the original data were presented otherwise, units of g C/m^2 and g N/m^2 ground area, respectively. If pretreatment data are available and substantial differences exist between treatment plots, observed values are corrected with the differences before calculating treatment effects. The correc-

tions are usually done with simple addition and subtraction unless additional information is available for linear model corrections (e.g., Lichter et al. 2005).

Analysis

We extracted mean and standard error (SE) of each treatment, from which the standard deviation (SD) is calculated as

$$\text{SD} = \text{SE}\sqrt{n} \qquad (1)$$

where n is the sample size. If data are given with a mean and a confidence interval (CI), the standard deviation is calculated as

$$\text{SD} = (\text{CI}_u - \text{CI}_l)\sqrt{n}/2Z_{\alpha/2} \qquad (2)$$

where CI_u and CI_l are the upper and lower limits of CI, and $Z_{\alpha/2}$ is Z score for a given level of significance equal to 1.96 when $\alpha = 0.05$ and 1.645 when $\alpha = 0.10$. In the cases where no standard errors, standard deviations, or confidence intervals are reported, we assigned standard deviations that are 1/10 of means. Although units of reported measurements are irrelevant for calculation of response ratios (Curtis 1996), we did separate plant- from area-based data. The latter is used to calculate the amount of C and N accumulated per unit of ground area.

The means in the treatment ($\bar{X}_t$) and control group ($\bar{X}_c$) are used to compute a response ratio by

$$\text{RR} = \ln(\bar{X}_t/\bar{X}_c) = \ln(\bar{X}_t) - \ln(\bar{X}_c). \qquad (3)$$

The natural log is used for the purpose of statistical tests. If $\bar{X}_t$ and $\bar{X}_c$ are normally distributed and both are greater than zero, $\ln(\bar{X}_t/\bar{X}_c)$ is approximately normally distributed (Curtis and Wang 1998) with a mean equal to the true response ratio and a variance (v) approximately equal to

$$v = \frac{s_t^2}{n_t \bar{X}_t^2} + \frac{s_c^2}{n_c \bar{X}_c^2} \qquad (4)$$

where n_t and n_c are the sample sizes for the treatment and control groups, respectively; s_t and s_c are the standard deviations for all comparisons in the treatment and control groups, respectively.

In this meta-analysis, we calculated a weighted response ratio (RR_{++}) from individual RR_{ij} ($i = 1, 2, \ldots, m; j = 1, 2, \ldots, k_i$) by giving greater weight to studies whose estimates have greater precision (lower v) so that the precision of the combined estimate and the power of the tests increase (Hedges and Olkin 1985, Gurevitch and Hedges 1999). Here m is the number of groups (e.g., different facilities or ecosystem types), k_i is the number of comparisons in the ith group. The weighted mean log response ratio (RR_{++}) is calculated by

$$\text{RR}_{++} = \frac{\sum\limits_{t=1}^{m} \sum\limits_{j=1}^{k_t} w_{ij}\text{RR}_{ij}}{\sum\limits_{i=1}^{m} \sum\limits_{j=1}^{k_t} w_{ij}} \qquad (5)$$

with the standard error as

$$s(\text{RR}_{++}) = \sqrt{\frac{1}{\sum\limits_{i=1}^{m} \sum\limits_{j=1}^{k_i} w_{ij}}} \qquad (6)$$

where w_{ij} is the weighting factor and is estimated by

$$w_{ij} = \frac{1}{v}. \qquad (7)$$

The 95% confidence interval for the log response ratio is

$$95\% \text{ CI} = \text{RR}_{++} \pm 1.96s(\text{RR}_{++}). \qquad (8)$$

The corresponding confidence limits for the response ratio can be obtained by computing their respective antilogs. If the 95% CI of a response variable overlaps with zero, the response ratio at elevated CO_2 is not significantly different from that at ambient CO_2. Otherwise, they are statistically different. The meta-analysis is conducted using the SAS program (SAS Institute 2003).

In addition to the significant test of response ratios (RR) for CO_2 treatment effects, we also plotted frequency distributions of RR to reflect variability of individual studies. The frequency distributions are assumed to follow normal distributions and fitted by a Gaussian function (i.e., normal distribution):

$$y = a \exp\left[-\frac{(x - \mu)^2}{2\sigma^2}\right] \qquad (9)$$

where x is the mean of RR in individual intervals, y is the frequency (i.e., number of RR values) in an interval, a is a coefficient showing the expected number of RR values at $x = \mu$, μ and σ are mean and variance of the frequency distributions of RR, and e is the base of exponent. We used the software Sigma Plot (Systat Software, Inc., Point Richmond, California, USA) for fitting Gaussian functions. The percentage of change in variables expressed in the text are estimated by ($e^{\text{RR}} - 1) \times 100\%$.

RESULTS

Changes in C pools in plant and soil

Averaged C pool sizes in shoot, root, and whole plant over the compiled database increase by 22.4%, 31.6%, and 23.0%, respectively, at elevated CO_2 in comparison with those at ambient CO_2 (Fig. 1, Table 1). This is consistent with results from other meta-analyses that biomass increases by approximately 30% at elevated CO_2 (Kimball et al. 1993). Averaged litter and soil C pool sizes are higher by 20.6% and 5.6%, respectively, at elevated relative to ambient CO_2 (Fig. 2). We calculated averaged C contents from all the ground-area-based data in our database, which are higher by approximately 110, 70, and 200 g C/m^2 at elevated than ambient CO_2 in plant, litter, and soil pools, respectively. The duration of exposure of those experimental plots
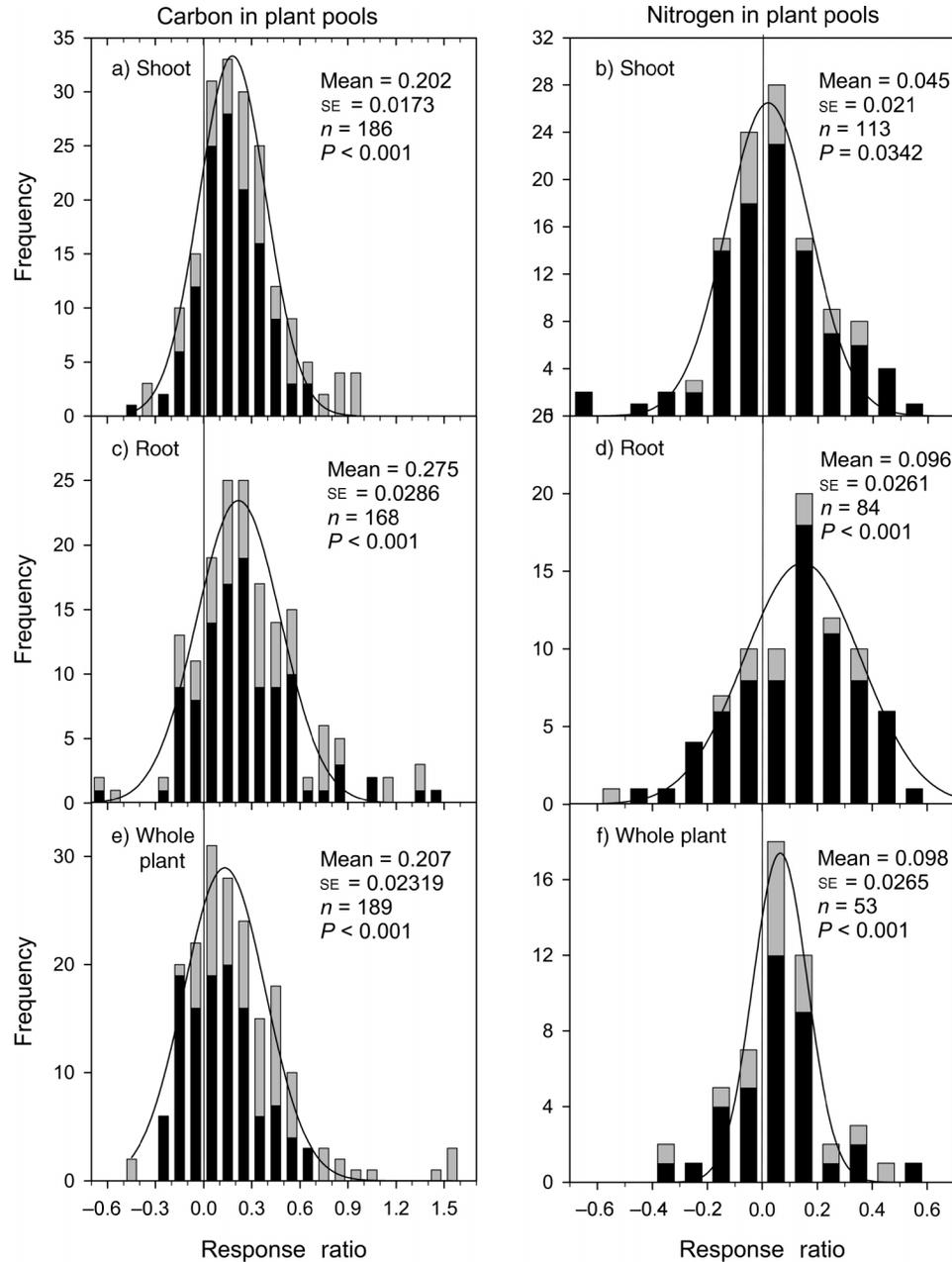
FIG. 1. Frequency distributions of response ratios (RR) of carbon and nitrogen pools in (a and b) shoot, (c and d) root, and (e and f) whole plants. The black part of bars indicates data points from ground-area-based measurements while the gray part of bars indicates data points from plant-based measurements. The solid line is the fitted Gaussian (normal) distribution to frequency data. The vertical lines were drawn at RR = 0.

to elevated CO_2 varies from one to eight years and is used to calculate annual rates of C accumulation. The averaged rate of C accumulation in ecosystems is approximately 100 g $C\cdot m^{-2}\cdot yr^{-1}$ more at elevated than ambient CO_2.

The increases in plant and soil C pool sizes vary with CO_2 experimental facilities, ecosystem types, and N treatments (Table 2). Elevated CO_2 using the FACE facility results in larger responses in belowground root C pool than other facilities while C contents in all the plant pools increase substantially at elevated CO_2 using growth chambers. Forest is generally the most responsive to elevated CO_2 in term of C accumulations in plant and soil pools whereas the wetland is the least responsive among the ecosystem types. Grassland significantly accumulates C in soil and belowground root pools. Additional N supply enhances effects of CO_2 on C accumulations in both plant and soil pools. Although

TABLE 1. Parameters of frequency distributions and fitted Gaussian (normal) distributions of response ratios (RR) of C pools, N pools, C:N ratio, and root:shoot ratio.

Variable	Sample size	Frequency distribution			Gaussian distribution		
		Mean	SE	P	a	σ	μ
ACP	186	0.202	0.017	<0.001	33.30	0.210	0.181
BCP	168	0.275	0.029	<0.001	23.44	0.263	0.219
WCP	189	0.207	0.023	<0.001	28.95	0.255	0.131
LCP	14	0.187	0.038	<0.001			
SCP	40	0.054	0.012	<0.001	9.95	0.082	0.057
ANP	113	0.045	0.021	<0.001	26.49	0.153	0.019
BNP	84	0.096	0.026	<0.001	15.52	0.211	0.144
WNP	53	0.098	0.027	<0.001	17.40	0.099	0.065
LNP	7	0.227	0.067	0.011			
SNP	36	0.106	0.032	0.002	13.22	0.093	0.050
A-C:N	57	0.110	0.021	<0.001	17.61	0.123	0.101
B-C:N	39	0.103	0.024	<0.001	13.33	0.107	0.088
L-C:N	8	0.026	0.036	0.490	3.03	0.108	0.038
S-C:N	36	0.028	0.011	0.015	17.71	0.082	0.035
R:S	76	0.067	0.0338	0.0524	16.59	0.162	0.026

Notes: P is the probability that the mean of RR equals zero. Parameters a, σ, and μ are defined in Eq. 9, and all differ statistically from zero. Abbreviations for C pools in aboveground shoot, belowground root, whole plants, litter, and soil are ACP, BCP, WCP, LCP, and SCP, respectively; N pools in aboveground shoot, belowground root, whole plant, litter, and soil are ANP, BNP, WNP, LNP, and SNP, respectively; C:N ratio in aboveground shoot and belowground root, litter, and soil are A-C:N, B-C:N, L-C:N, and S-C:N, respectively; and root:shoot ratio is abbreviated R:S.

duration of CO_2 exposure is a major factor that determines the amounts of accumulated C in ecosystems (Idso 1999), our analysis did not show significant correlations of any of the 18 variables in question with exposure time, due to high variability in baseline data in control plots among ecosystems.

Changes in N pools in plant and soil

In association with net C accumulations, N contents in plant and soil pools significantly increase at elevated CO_2. Averaged N pool sizes in shoot, root, and whole plant over the database are 4.6%, 10.0%, and 10.2%, respectively, higher at elevated than ambient CO_2 (Fig. 1). Averaged litter and soil N contents also increase by 25.4% and 11.2%, respectively, at elevated CO_2 in comparison with those at ambient CO_2 (Fig. 2). We averaged area-based data to estimate N accumulations in plant and soil pools. Averaged N contents increase by 1.75, 3.17, and 1.87 g N/m^2 in plant, litter, and soil pools, respectively, at elevated CO_2 relative to those at ambient CO_2. Thus, the averaged increase in the whole ecosystem N content is 6.77 g N/m^2 and an averaged annual rate of ecosystem N accumulation is approximately 1.0 g $N \cdot m^{-2} \cdot yr^{-1}$ more at elevated than ambient CO_2.

Nitrogen accumulations in plant and soil pools also vary with CO_2 experimental facilities, ecosystem types, and N treatments (Table 2). Averaged N contents in plant pools increase more in elevated CO_2 plots using FACE than open-top chambers (OTC) or growth chambers (GC). CO_2 treatments with OTC result in a larger increase in the soil N pool size than with FACE. Among the ecosystem types, CO_2-induced N accumulations are higher in forests and grasslands than in deserts and wetlands. Averaged N accumulations in all the plant pools at elevated CO_2 are statistically significant regardless of N treatments. However, the averaged soil N pool at elevated CO_2 significantly increases with additional N supply but decreases in the control plots of N treatments in comparison to that at ambient CO_2.

Flexibility in C:N ratio and R:S ratio

The CO_2-induced percent increases in C contents in plant pools are larger than the increases in plant N pools (Fig. 1), resulting in significant increases in C:N ratios in all the plant pools. Averaged C:N ratios in shoot and root pools over the entire database increase by 11.6% and 10.8%, respectively, at elevated CO_2 in comparison to those at ambient CO_2 (Fig. 3). Averaged soil C:N ratio is also higher by 2.9% at elevated than ambient CO_2 in spite of the percent increase averaged over RR values of soil C pools is smaller than that of the soil N pools (Fig. 2c and d). This mismatch between changes in C:N ratio and changes in C and N contents occurs because the meta-analysis uses different sets of data in computation of averaged changes in RR. However, the estimated mean changes (i.e., μ values) from fitted Gaussian equations are 0.057 and 0.050 for soil C and N contents, respectively, which is logically consistent with the mean change of 0.035 in soil C:N ratio (Table 1). In addition, CO_2-induced change in litter C:N ratio is not statistically significant. The averaged change in R:S ratio in response to elevated CO_2 is marginally significant (Fig. 4), similar to results from other studies (e.g., Rogers et al. 1996).

Forest, on average, is more flexible in adjusting C:N ratios than the other ecosystems in response to elevated CO_2 (Table 2). CO_2-induced increases in C:N ratio are
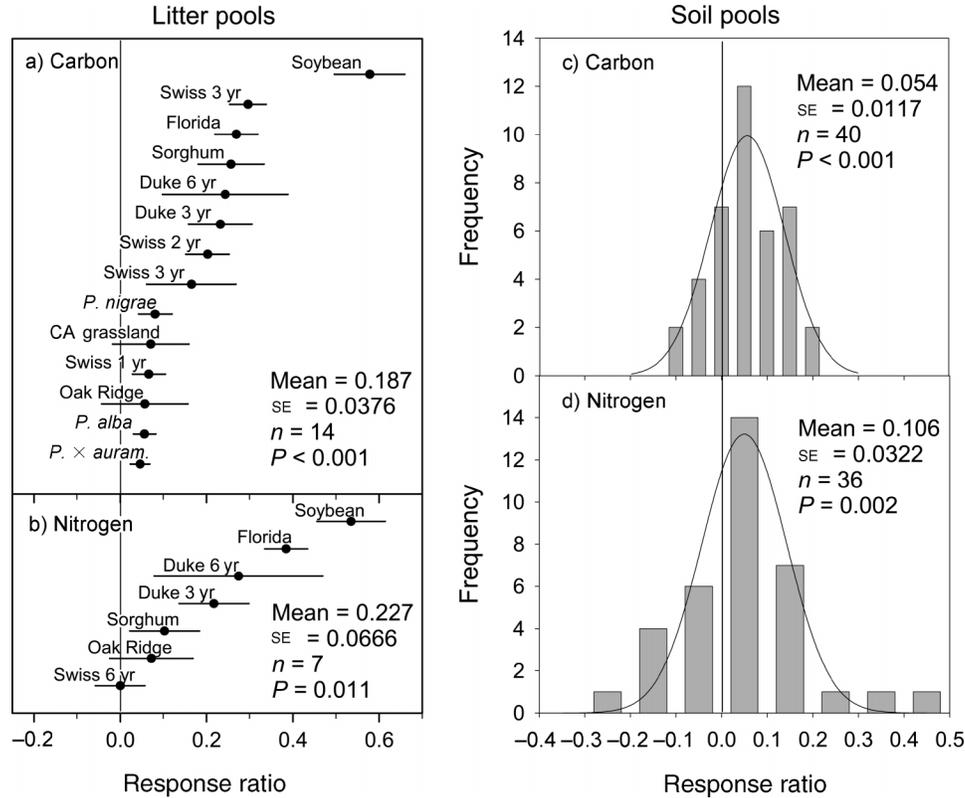
FIG. 2. Response ratios (RR, mean ± SE for each data set) of (a) litter C pools and (b) litter N pools, and frequency distributions of response ratios for (c) soil C and (d) soil N pools. Solid lines in (c) and (d) are fitted Gaussian distributions to frequency data; vertical lines are drawn at RR = 0. Data in (a) and (b) are from Torbert et al. (2000) for soybean and sorghum (experiment using open-top chambers (OTC) in Auburn, Alabama, USA); Niklaus et al. (2001) for Swiss 3 yr, Niklaus et al. (2003) for Swiss 6 yr, Leadley et al. (1999) for Swiss 1 yr, 2 yr, and 3 yr (OTC experiment in a grassland in Switzerland); Johnson et al. (2003) for Florida (OTC experiment in an oak woodland in Florida, USA); Lichter et al. (2005) for Duke 6 yr; Schlesinger and Lichter (2001) for Duke 3 yr (free-air CO_2 enrichment [FACE] experiment in the Duke loblolly pine forest in North Carolina, USA); Calfapietra et al. (2003) for *P. nigra*, *P. alba*, and *P. × auramericana* (pure stands of the three species used in a FACE experiment in Italy); Higgins et al. (2002) for CA grassland (OTC experiment in California, USA); Johnson et al. (2004) for Oak Ridge (FACE experiment in the sweetgum forest in Oak Ridge, Tennessee, USA).

TABLE 2. Response ratios (×100) of C contents, N contents, and C:N in various plant and soil pools under different facilities, ecosystems types, and nitrogen treatments. See Table 1 for the abbreviations of variables.

Variable	Facility			Ecosystem type					Nitrogen treatment	
	FACE†	OTC‡	GC§	Cropland	Forest	Grassland	Desert	Wetland	Control	+N
ACP	11.59*	13.87*	16.22*	14.21*	21.50*	9.80*	9.66	3.43	2.98	22.42*
BCP	47.23*	1.33	36.47*	22.54*	48.76*	40.49*	11.4	−12.97*	38.98*	51.96*
WCP	4.57*	7.94*	21.22*	15.72*	26.72*	0.54	24.60*	−8.51	12.26*	28.35*
SCP	5.75*	6.62*		2.81	5.56*	10.49*		−0.73	−4.28	13.35*
ANP	21.11*	12.58*	4.35	−1.6	31.28*	20.46*	2.9	−10.5*	20.45*	31.02*
BNP	27.73*	19.41*	12.27*		24.49*	26.76*	−3.64	−0.60	14.07*	30.73*
WNP	26.25*	12.80*	14.66*		15.08*	25.67*	−0.91	8.98*	24.90*	27.71*
SNP	3.52	11.52*			18.29*	5.71*		−8.52	−9.18*	13.35*
A-C:N	9.79*	11.47*	5.70*		15.22*	11.05*		8.69	12.13*	7.84
B-C:N	4.90*	10.86*	4.34*		14.02*	5.46*		9.29	7.99	5.64
S-C:N	0.74	1.88*			1.26	1.67	0.39		−1.63	−1.90
R:S	4.90*	10.35*	4.35*		14.01*	5.46*		9.29	7.99	5.64

* $P < 0.05$.
† FACE, free-air CO_2 enrichment.
‡ OTC, open-top chamber.
§ GC, greenhouse.
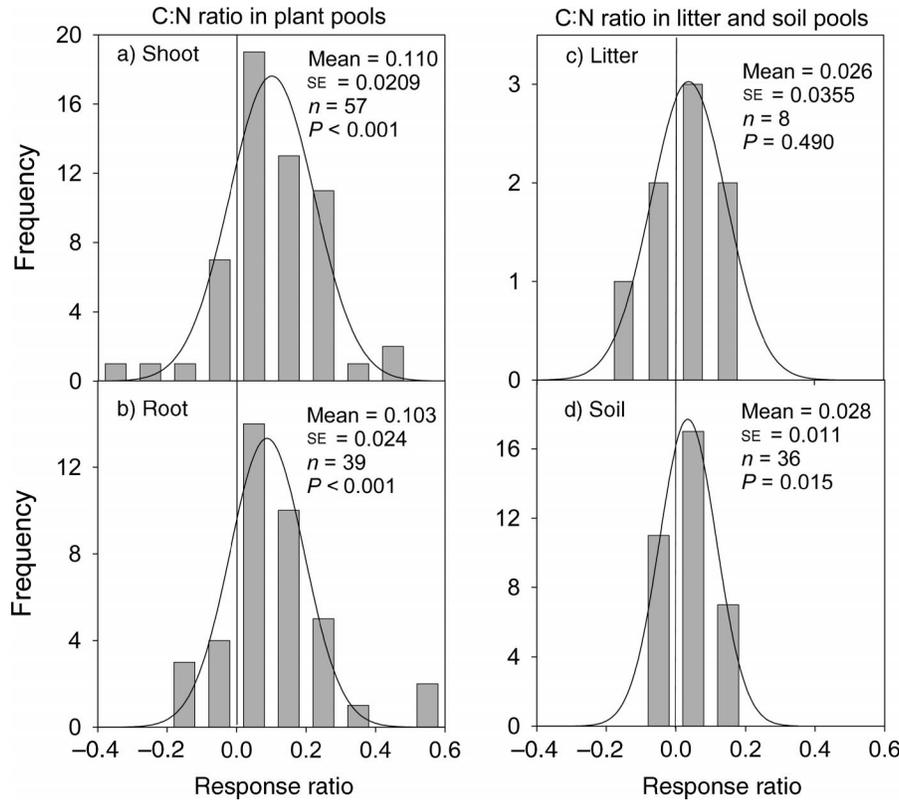
FIG. 3. Frequency distributions of response ratios (RR) of carbon:nitrogen (C:N) ratios in (a) shoot, (b) root, (c) litter, and (d) soil. The solid line is the fitted Gaussian distribution to frequency data; the vertical lines is drawn at RR = 0.

much higher in aboveground shoot than in belowground root and soil regardless of CO_2 experimental facilities, ecosystem types, and nitrogen treatments. Although the CO_2-induced change in soil C:N ratio averaged over all the studies is statistically significant, none of the changes except with OTC is significant

FIG. 4. Frequency distribution of response ratios (RR) of root:shoot ratios. The solid line is the fitted Gaussian distribution to frequency data; the vertical lines is drawn at RR = 0.

when evaluated under different facilities, ecosystem types, or N treatments (Table 2) due to smaller sample sizes. Averaged R:S ratio is more responsive to elevated CO_2 using OTC than the other experimental facilities and more responsive in forest than in the other ecosystems.

Among the 18 variables evaluated in this study, variability among different studies as measured by the σ value in Table 1 is highest for belowground root C content and lowest for soil C:N ratio and soil C pool sizes. Variability is also very high for aboveground shoot C content, whole plant C content, and belowground root N content. The low-variability variables include soil N pool sizes and whole plant N content.

DISCUSSION

Our results indicate that C and N contents in all the plant and soil pools significantly increase, leading to more net C and N accumulations in ecosystems at elevated than ambient CO_2. The CO_2-induced net accumulations of C and N contents in ecosystems at least suggest that complete down-regulation of CO_2 stimulation of plant growth and other C processes is not pervasive across ecosystems. The net N accumulation likely supports long-term C sequestration in response to rising atmospheric CO_2 concentration. Our meta-analysis also reveals that CO_2-induced changes in C

and N pools are highly variable among studies. The high variability reflects diverse responses of various C and N processes to elevated CO_2. Despite the variability, the CO_2 effects on ecosystem C and N contents can be detected in this study largely because meta-synthesis increases statistical power of significance test. The net C and N accumulations revealed in this study, together with studies of C and N dynamics during succession over hundreds to millions of years (Vitousek 2004), suggest that ecosystems may have intrinsic capabilities to stimulate N accumulation by C input.

Net carbon and nitrogen accumulations at elevated CO_2

Accumulation of organic C in plants and soil as demonstrated in this study may result from several processes. These processes include increased C input into ecosystems, decreased litter quality and decomposability, and enhanced physical protection through formation of either intra-aggregate or organomineral complexes. Rising atmospheric CO_2 concentration by 200–350 ppm generally stimulates photosynthetic C fixation by 30–70% (Luo and Mooney 1996). As a consequence, plant biomass growth and C input into ecosystems increase by an average of approximately 30% (Kimball et al. 1993) (Fig. 1). A meta-synthesis indicates that elevated CO_2 generally does not alter litter quality (Norby et al. 2001) and consequently may not affect decomposition rates of litter. Increased C input into soil (Zak et al. 2000) (Fig. 2a) and mycorrhizal growth at elevated CO_2 probably enhance protection of organic matter in soil aggregates from microbial decomposition (Rillig 2004).

Ecosystems have a number of processes that can lead to net N accumulation under elevated CO_2. Those processes include biological N fixation, retention of atmospheric N deposition, reduced N loss in gaseous and liquid forms, and extended root growth to root-free zones for N uptake (Luo et al. 2004). The increase in R:S ratio (Fig. 4), combined with increases in biomass growth of both roots and shoots (Fig. 1a and b), presumably results in expansion of rooting systems at elevated CO_2. The expanded rooting systems may take up nutrients from soil zones that may not be exploited by roots at ambient CO_2. Biological N fixation is stimulated in many studies (Dakora and Drake 2000, Cheng et al. 2001) but either does not change or even decreases in other studies (Billings et al. 2002, Hungate et al. 2004) at elevated CO_2 compared to that at ambient CO_2. Elevated CO_2 usually stimulates plant N uptake and decreases standing pools of inorganic N, leading to decreased ammonia volatilization and nitrate leaching (Reich et al. 2001, Mosier et al. 2002). Other processes, such as increased soil water content (Hungate et al. 2002, Schäfer et al. 2002) and limitations imposed by other nutrient elements (Hungate et al. 2004), may result in decreased N fixation or increased N losses.

Such diverse responses are reflected by the variability of frequency distributions in Figs. 1–3. Nevertheless, the averaged N contents in all the plant, litter, and soil pools significantly increase at elevated CO_2 compared with those at ambient CO_2.

In all the studies compiled in our database, litter C and N pool sizes consistently increase at elevated CO_2 (Fig. 2a and b). CO_2-induced changes in C and N contents in other pools, however, vary from increases in some studies to decreases in other studies (Fig. 1 and Fig. 2c and d). Overall, the percent increases in C contents (Fig. 1a, c, and e) are larger than the percent increases in N contents in all the three plant pools (Fig. 1b, d, and f). In contrast, the percentage of increase in soil C content (Fig. 2c) is smaller than the percentage of increase in soil N content (Fig. 2d). Whether the contrasting changes between soil and plant pools result purely from sampling errors in the meta-synthesis or signify any fundamental ecological principles is yet to be carefully examined. In nature, N is fixed in soil and translocated to plant whereas C is synthesized in plant and transferred to soil. Thus, it is conceivable that elevated CO_2 stimulates more C than N accumulations in plant pools but conversely more N than C accumulations in soil pools.

Long-term stimulation of C sequestration by elevated CO_2

One of the most crucial issues in global change ecology is how long CO_2 stimulation of plant growth and C sequestration would last (Luo et al. 2003). Cases have been reported on either complete, partial, or no down-regulation of CO_2 stimulation of photosynthesis, plant growth, or other C processes (Long et al. 2004, Nowak et al. 2004). It has been widely suggested that the CO_2 stimulation of plant growth and C sequestration is regulated by N availability (Luo et al. 1994, Field 1999, Oren et al. 2001). Modeling studies (e.g., Rastetter et al. 1997) suggest that the CO_2 stimulation of C processes is primarily regulated by redistribution of N among plant and soil pools on a time scale of years or shorter. The long-term CO_2 stimulation of ecosystem C sequestration on a time scale of decades or longer relies on increases in total ecosystem N stocks (Rastetter et al. 1997, 2005, Luo et al. 2004). While it is unlikely that ecosystem CO_2 experiments would last for decades, this meta-analysis provides a critical assessment on N stocks in plant and soil pools, which are the key parameters to indicate long-term C sequestration.

The significant net N accumulations revealed in this meta-analysis, at the minimum, suggest that complete down-regulation of CO_2 stimulation of ecosystem C processes would not be pervasive across ecosystems. If the long-term C sequestration is indeed regulated primarily by N availability, the substantial N accumulations in all the plant, litter and soil pools at elevated CO_2 would support long-term C sequestration in

terrestrial ecosystems in response to rising C_a. Adjustments in C:N ratios in the plant, litter and soil pools (Fig. 3), redistribution of ecosystem N stocks among the pools, and increased rooting systems (Fig. 4) likely support short-term CO_2 stimulation of plant growth and C sequestration. Concomitant increases in C and N contents in plant and soil pools at elevated CO_2 as shown in this study point toward a long-term trend of terrestrial C sequestration in response to rising C_a.

The meta-analysis conducted in this study could not precisely assess to what extent C sequestration in ecosystems is constrained by N availability at elevated CO_2. Photosynthetic C fixation rate can instantaneously respond to elevated CO_2 with a 20–70% increase when the ambient CO_2 concentration increases by 200–350 ppm. But changes in the C and N pool sizes are cumulative and presumably increase gradually from 0% in the very beginning of a CO_2 experiment until the pool sizes are fully equilibrated to the new state of elevated CO_2 (Luo and Reynolds 1999). Therefore, the magnitudes of increases in pool sizes would not equal those in flux rates. But the smaller percent increases in plant N pools than in plant C pools and the increased C:N ratios could suggest that rising C_a primarily stimulates ecosystem C storage followed by N accumulation with time lags. Also, additional N fertilization in CO_2 experiments results in larger stimulation of C accumulations than no N addition treatments (Table 2). Thus, three lines of evidence likely indicate that N at least partially constrains C accumulation in the CO_2 experiments. Nevertheless, N is less likely to constrain C accumulation in the real-world ecosystems, which are exposed to a gradual increase in C_a and require much less N to balance additional C influx than in CO_2 experimental plots (Luo and Reynolds 1999).

Long-term coupling between C and N cycles in terrestrial ecosystems

The net N accumulation revealed in this study is consistent with results from other studies on long-term C and N processes. N accumulations in ecosystems have long been documented in association with C accumulations during both primary and secondary successions (Crocker and Major 1955, Binkley et al. 2000, Vitousek 2004). The rate of N accumulation in soil pools varies with ecosystems and can reach 5 g $N \cdot m^{-2} \cdot yr^{-1}$ or more. For example, the rate of N accumulation is 0.83 g $N \cdot m^{-2} \cdot yr^{-1}$ in the mineral soil during the alder-tree stage of the primary succession at Glacial Bay, Alaska (Chapin et al. 1994). During the same stage, the rate of the C accumulation is 80 g $C \cdot m^{-2} \cdot yr^{-1}$. Along a chronosequence of 10-, 50-, and 142-yr-old 'a'a lava flows on Mauna Loa, Hawaii, total N content is 4.8, 10.9, and 85.7 g N/m^2, respectively, while the mass of organic matter are 600, 2200, and 7600 g/m^2 (Crews et al. 2001). The mean rate of N accumulation is between 0.2–0.31 g $N \cdot m^{-2} \cdot yr^{-1}$. During a secondary succession over 15 years after harvesting at the Walker

Branch watershed, Tennessee, Johnson and Todd (1998) observed that rate of N accumulation is as high as 5.3–8.0 g $N \cdot m^{-2} \cdot yr^{-1}$.

The close coupling between C and N cycles during ecosystem development over the earth history (Vitousek 2004) and under elevated CO_2 suggests that C and N processes are mutually regulated by each other. Although the past research in the CO_2 research community has focused on regulation of C processes by soil N availability, regulation of N fixation and loss processes by C input under elevated CO_2 is indeed an equally important issue in global change ecology that has to be carefully examined. The close coupling between C and N cycles also must be considered when we predict C sequestration in future global change scenarios.

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APPENDIX A

A list of papers from which the data were extracted for this metadata analysis (*Ecological Archives* E087-001-A1).

APPENDIX B

A table of variables extracted from each of the papers (*Ecological Archives* E087-001-A2).

SPECIAL FEATURE