

# Carbon and nitrogen dynamics during forest stand development: a global synthesis

Yuanhe Yang<sup>1</sup>, Yiqi Luo<sup>1</sup> and Adrien C. Finzi<sup>2</sup>

<sup>1</sup>Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA; <sup>2</sup>Department of Biology, Boston University, Boston, MA 02215, USA

## Summary

Author for correspondence:

Yuanhe Yang

Tel: + 1 405 325 8578

Email: yhyang@ou.edu

Received: 25 October 2010

Accepted: 3 January 2011

*New Phytologist* (2011) **190**: 977–989

doi: 10.1111/j.1469-8137.2011.03645.x

**Key words:** carbon accumulation, carbon–nitrogen interactions, disturbance, forest ecosystems, mineral soil, nitrogen accretion, nitrogen capital, stand age.

- Our knowledge of carbon (C) and nitrogen (N) dynamics during stand development is not only essential for evaluating the role of secondary forests in the global terrestrial C cycle, but also crucial for understanding long-term C–N interactions in terrestrial ecosystems. However, a comprehensive understanding of forest C and N dynamics over age sequence remains elusive due to the diverse results obtained across individual studies.

- Here, we synthesized the results of more than 100 studies to examine C and N dynamics during forest stand development.

- Our results showed that C accumulated in aboveground vegetation, litter and forest floor pools, while the mineral soil C pool did not exhibit significant changes in most studies. The rate of C changes declined with stand age and approached equilibrium during the later stage of stand development. The rate of N changes exhibited linear increases with that of C changes, indicating that N also accrued in various ecosystem components except mineral soil.

- These results demonstrate that substantial increases in C pools over age sequence are accompanied by N accretion in forest ecosystems. The concurrent C and N dynamics suggest that forest ecosystems may have an intrinsic ability to preclude progressive N limitation during stand development.

## Introduction

Secondary forests, regenerated on abandoned agricultural land and pasture or re-established after stand-replacing disturbances, are an important component of terrestrial ecosystems around the world (Kauppi *et al.*, 2006). Secondary forests have the potential to sequester a large amount of carbon (C) because of their rapid regrowth following disturbance (Houghton *et al.*, 2009). However, the role of secondary forests in the global terrestrial ecosystem C cycle remains uncertain, partly because of the lack of explicit algorithms for stand-replacing disturbances in land surface models (Running, 2008). Moreover, it remains controversial whether secondary forests could continue to sequester C during the later stage of stand development: old-growth forests have been considered to be C neutral (Odum, 1969), while recent studies have reported that old-growth forests could function as a C sink (Zhou *et al.*, 2006; Luysaert *et al.*, 2008). In addition, soil C dynamics in secondary forests remain poorly characterized (Peltoniemi

*et al.*, 2004) although vegetation has been widely accepted to be a C sink during stand development (Johnson *et al.*, 2000; Silver *et al.*, 2000). Given that soil is the largest C pool in the terrestrial biosphere, soil C dynamics may exert significant effects on the ecosystem C balance (Davidson & Janssens, 2006). It has been suggested that substantial C release from soil may even offset C sequestration in vegetation (Bellamy *et al.*, 2005). Therefore, to accurately evaluate their contributions to the global terrestrial ecosystem C cycle, a comprehensive assessment of C dynamics in both vegetation and soil is essential for secondary forests around the world (Law *et al.*, 2001; Houghton *et al.*, 2009).

Terrestrial carbon–nitrogen (C–N) interactions have attracted considerable interest because of their importance in determining whether the C sink in land ecosystems (e.g. C accumulation in secondary forests) could be sustained over the long term (Strain & Bazzaz, 1983; Finzi *et al.*, 2001; Hungate *et al.*, 2003; Luo *et al.*, 2006b; Reich *et al.*, 2006). It has been suggested that the change in ecosystem nitrogen (N) capital (i.e. the amount of N) is a key

parameter regulating long-term terrestrial C sequestration (Rastetter *et al.*, 1997; Luo *et al.*, 2004). Specifically, modeling studies demonstrated that N capital in an ecosystem determined the long-term trend of terrestrial C sink (Rastetter *et al.*, 1997). If a land surface model allows increased N input into an ecosystem, C sequestration in land ecosystems will be sustainable (Rastetter *et al.*, 1997). Similarly, a conceptual framework of progressive N limitation also predicted that N would increasingly constrain terrestrial C dynamics only if ecosystem N capital did not change over time (Luo *et al.*, 2004). If additional C inputs stimulate the capital gain of N through biological fixation and atmospheric deposition, increased uptake for soil available N or decreased N losses, progressive N limitation will not occur (Luo *et al.*, 2006a). However, current evidence on terrestrial C–N interactions comes primarily from short-term carbon dioxide (CO<sub>2</sub>) enrichment experiments (e.g. Finzi *et al.*, 2006; Hungate *et al.*, 2006; Norby & Iversen, 2006) which usually do not last long enough to permit quantification of the changes in ecosystem N capital. Thus, to improve our understanding of C–N interactions in terrestrial ecosystems, it is critical to use long-term data series, such as those obtained in secondary forests, to determine the changes occurring in ecosystem N capital (Rastetter *et al.*, 1997; Luo *et al.*, 2004; Johnson, 2006).

During the past several decades, numerous studies have been conducted to quantify the changes in both C (e.g. Law *et al.*, 2001; Gough *et al.*, 2007) and N (e.g. Zak *et al.*, 1990; Knops & Tilman, 2000) stocks during forest stand development. However, the experimental results obtained

in different studies are highly variable. For instance, O'Neill *et al.* (2006) observed that C accumulated in mineral soil in black spruce (*Picea mariana*) stands in the interior of Alaska after fire disturbance, whereas Rothstein *et al.* (2004) documented significant loss of soil C in Michigan jack pine (*Pinus banksiana*) forests along a 72-yr wildfire chronosequence. In addition, the C pool in mineral soil has also been reported to exhibit an initial decrease and a subsequent increase (Zak *et al.*, 1990) or a statistically insignificant change (Perez *et al.*, 2004; Gough *et al.*, 2007) during forest stand development. The inconsistent results obtained in different studies indicate that a comprehensive understanding of forest C and N dynamics over age sequence remains elusive.

The highly diverse results from individual studies are unlikely to reveal a generalized pattern that can be applied to various forest ecosystems around the world (Lu *et al.*, 2010). However, the results can be synthesized across individual studies to examine the probability of changes in ecosystem C and N pools over age sequence (Carpenter *et al.*, 2009). This study was designed to examine C and N dynamics during forest stand development through the compilation and analysis of published data from 124 individual studies. Specifically, we used the synthesized data sets to examine ecosystem C dynamics along the age gradient; to investigate the relationship between the rate of C pool change and biophysical factors (e.g. stand age and climatic variables); to explore the relationship between the rate of N pool change and the rate of C pool change over age sequence; and to quantify the changes in ecosystem N capital during stand development.

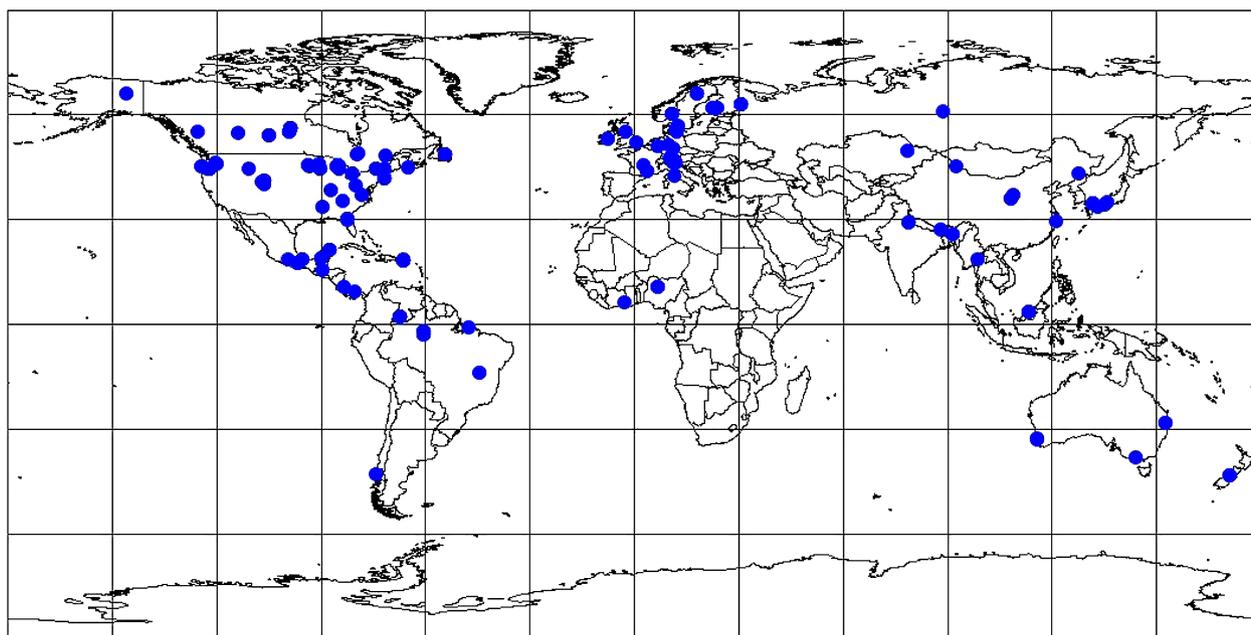


Fig. 1 Locations of various individual studies included in this synthesis. Some individual studies contain multiple age sequences.

## Materials and Methods

### Data compilation

We compiled a database of 124 published papers from the literature that reported C and N dynamics during forest stand development (Fig. 1, Supporting Information Notes S1, Table S1). To avoid bias in reference selection, we collected data on C and N pools and C : N ratio based on the following three criteria: the study must focus on C and/or N pools in forest ecosystems during stand development; each sequence must include at least five data points to allow detection of statistical trends in C and N pools and C : N ratio along the age gradient; and each sequence must contain quantitative information on stand age. In addition, those papers that evaluated forest C and N dynamics over age sequence primarily based on ecosystem models were not included.

The raw data were either extracted from published tables or obtained by digitizing published graphs using ORIGINPRO 7.5 (OriginLab, Northampton, MA, USA). The entire database was comprised of *c.* 2400 entries, each containing geographic location (longitude and latitude), climatic information (mean annual temperature (MAT) and mean annual precipitation (MAP)), disturbance type (fire, harvest, agricultural abandonment or plantation), forest type (boreal, temperate or tropical forest or plantation), stand age and 18 target variables. These 18 variables described C pools, N pools and C : N ratios in aboveground vegetation (including both leaves and woody tissues), leaves, woody tissues, litter, forest floor and mineral soil. All original data on C and N stocks were converted to standard units (Mg C ha<sup>-1</sup> or Mg N ha<sup>-1</sup>). If necessary, a conversion factor of 0.5 was used to estimate vegetation C pool size from a given oven-dry biomass (Pregitzer & Euskirchen, 2004). Soil C and N contents were estimated in some cases when C and N concentrations and bulk density were provided. Similarly, the C : N ratio was calculated if data on C and N pools were synchronously available. In addition, data on MAT and MAP were either extracted from each publication or obtained from a global climate database (<http://www.worldclim.org/>) according to longitude and latitude (Hijmans *et al.*, 2005).

To increase the comparability of data derived from different studies, the original soil C data were converted to the soil C pool in the top 100 cm using the depth functions developed by Jobbágy & Jackson (2000) (Eqns 1–2). Specifically, the changes in soil C pool along the soil profile were described by an asymptotic function (Eqn 1). Based on vertical distributions of the soil C pool in forest ecosystems around the world (Jobbágy & Jackson, 2000), the parameter  $\beta$  in Eqn 1 was calculated to be 0.97. The soil C pool in the upper 100 cm could then be estimated from the original soil C pool using Eqn 2. In a similar fashion, the original soil N data were converted to the soil N pools in

the top 100 cm using the depth distributions provided by Jobbágy & Jackson (2001).

$$Y = 1 - \beta^d \quad \text{Eqn 1}$$

$$\text{SOC}_{100} = \frac{1 - \beta^{100}}{1 - \beta^{d_0}} \text{SOC}_{d_0}, \quad \text{Eqn 2}$$

$Y$ , the cumulative proportion of the soil C pool from the soil surface to depth  $d$  (cm);  $\beta$ , the relative rate of decrease in the soil C pool with soil depth (Jobbágy & Jackson, 2000);  $\text{SOC}_{100}$ , the soil C pool in the upper 100 cm (Mg C ha<sup>-1</sup>);  $d_0$ , the original soil depth available in individual studies (cm);  $\text{SOC}_{d_0}$ , the original soil C pool (Mg C ha<sup>-1</sup>).

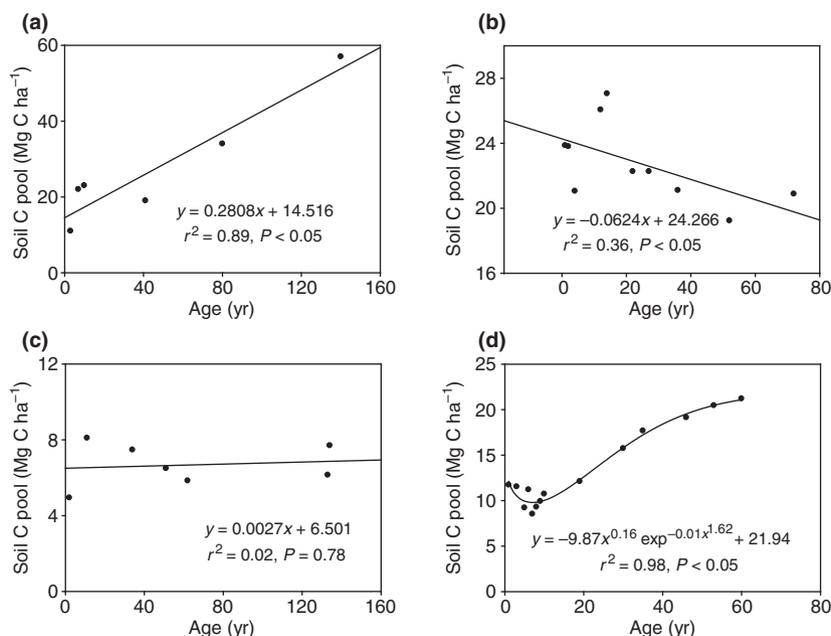
### Data analyses

Data were processed in the following three steps. First, we examined the dynamics of C and N pools and C : N ratios along the age gradient. Both vegetation C and N pools are usually hypothesized to show a linear increase and then approach a plateau during forest stand development (Odum, 1969). However, in this synthesis, both vegetation C and N pools exhibited linear changes but did not level off in most cases. For instance, the C pool in aboveground vegetation did not approach a plateau in 97% of individual studies, possibly as a consequence of the short experimental duration of these individual studies (Johnson *et al.*, 2000). The changes in soil C and N pools during stand development are expected to exhibit an initial decrease and a subsequent increase over age sequence, which can be characterized with a gamma function (Covington, 1981; Zak *et al.*, 1990). Thus, either a linear function (Eqn 3) or a gamma function (Eqn 4) was used to fit the relationships of ecosystem C and N pools with stand age. The best fit was determined as the function producing the smallest residual mean square, with the significance level at  $P < 0.05$  (Zak *et al.*, 1990). We then grouped age-related C and N dynamics into one of four patterns: increase (O'Neill *et al.*, 2006), decrease (Rothstein *et al.*, 2004), no trend (Perez *et al.*, 2004) or Covington curve (Zak *et al.*, 1990) (Fig. 2). The Covington curve was fitted by a gamma function (Eqn 4), characterized by an initial decrease and a subsequent increase in C pool over age sequence (Covington, 1981; Zak *et al.*, 1990).

$$y = ax + b \quad \text{Eqn 3}$$

$$y = ax^b \exp^{cx^d} + e \quad \text{Eqn 4}$$

$x$ , stand age (yr);  $y$ , C or N content (Mg ha<sup>-1</sup>);  $a$ ,  $b$ ,  $c$ ,  $d$  and  $e$ , statistical coefficients (Covington, 1981; Zak *et al.*, 1990).



**Fig. 2** Age-related changes in the soil carbon (C) pool during forest stand development. (a) Increase (O'Neill *et al.*, 2006), (b) decrease (Rothstein *et al.*, 2004), (c) no trend (Perez *et al.*, 2004) and (d) Covington curve (Zak *et al.*, 1990).

Second, we explored the associations between the rate of absolute N change and the rate of absolute C change for various ecosystem components. Given that both C and N pools exhibited linear changes in most cases, the rate of absolute C change over age sequence was determined as the slope of the relationship between C pool and stand age within each sequence and calculated through the ordinary least squares (OLS) regression ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ). The rate of absolute N change over age sequence was obtained in a similar manner ( $\text{Mg N ha}^{-1} \text{ yr}^{-1}$ ). In addition, we also examined the relationships between the rate of absolute C change and biophysical factors, such as stand age and climatic variables.

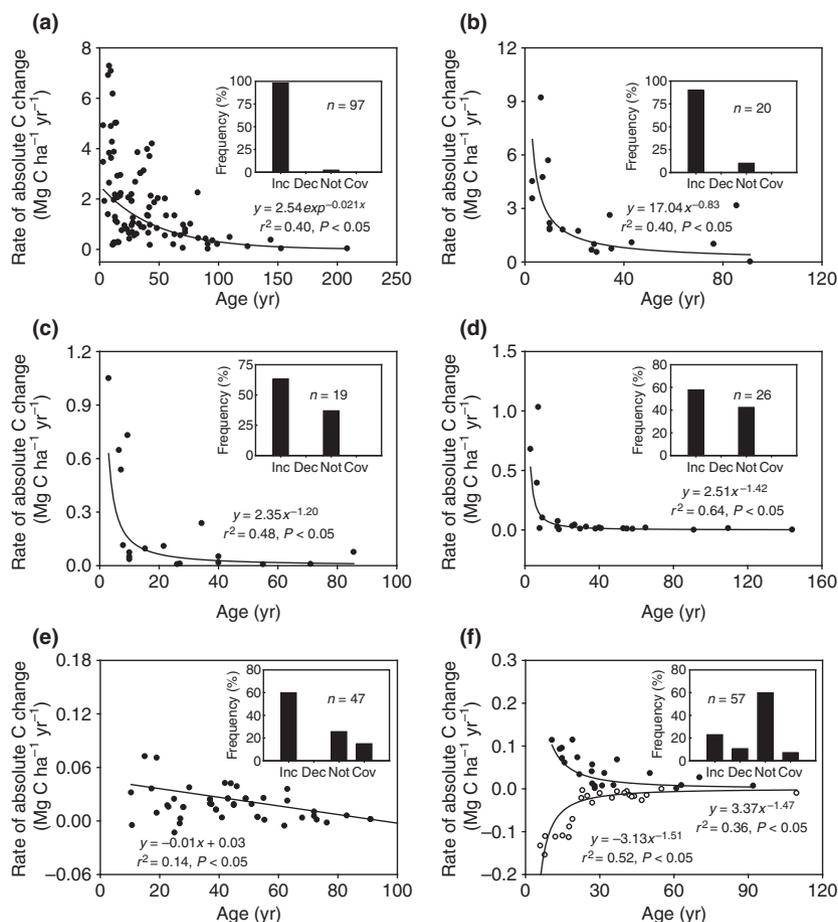
Third, to further elucidate C–N interactions during stand development, we investigated the relationship between the rate of relative N change and the rate of relative C change for various ecosystem components. The relative C and N changes were used to remove the effects of pool sizes on the rates of C and N changes over age sequence. The relative C change was defined as the C pool at the current age stage divided by the C pool at the previous age stage for each sequence. The rate of relative C change (per year) was then calculated as the relative change in the C pool divided by the age interval between the two adjacent age stages. The rate of relative N change (per year) was determined in a similar manner. All statistical analyses were conducted using the software package R (R Development Core Team, 2007).

## Results

C pools in various ecosystem components showed different trends along the age gradient (Fig. 3). For aboveground

vegetation, woody tissue, leaf, litter and forest floor C pools, an increasing trend was the most frequently observed pattern (Fig. 3a–e). Although the increasing pattern occurred in approximately one-fifth of the individual studies, a statistically insignificant trend predominated for soil C dynamics over age sequence (Fig. 3f). Interestingly, the rates of C pool changes declined with stand age and approached an equilibrium state (i.e. C flux was near zero) in aboveground vegetation ( $r^2 = 0.40$ ,  $P < 0.05$ ), woody tissues ( $r^2 = 0.40$ ,  $P < 0.05$ ), leaves ( $r^2 = 0.48$ ,  $P < 0.05$ ), litter ( $r^2 = 0.64$ ,  $P < 0.05$ ) and the forest floor ( $r^2 = 0.14$ ,  $P < 0.05$ ) (Fig. 3a–e) during the later stage of stand development. The rate of C accumulation and loss in mineral soil exhibited opposite patterns with respect to stand age (Fig. 3f). However, the absolute value of the rate of soil C pool change declined with stand age and tended to be at equilibrium under both scenarios ( $r^2 = 0.36$ ,  $P < 0.05$  for C accumulation;  $r^2 = 0.52$ ,  $P < 0.05$  for C loss). In addition, the rate of C pool change was also closely correlated with climatic variables (Table 1). Specifically, the rate of C accumulation in aboveground vegetation was positively associated with both MAT ( $r = 0.33$ ,  $P < 0.05$ ) and MAP ( $r = 0.21$ ,  $P < 0.1$ ). Also, the rate of C pool change in the forest floor exhibited positive correlations with both MAT ( $r = 0.70$ ,  $P < 0.001$ ) and MAP ( $r = 0.44$ ,  $P < 0.05$ ) (Table 1). By contrast, climatic factors had weak relationships with the rate of soil C pool change over age sequence (MAT:  $r = 0.11$ ,  $P = 0.52$ ; MAP:  $r = 0.10$ ,  $P = 0.54$ ) (Table 1).

The rate of absolute N change increased linearly with that of C pool change in aboveground vegetation ( $r^2 = 0.95$ ,



**Fig. 3** Relationships between the rate of absolute carbon (C) change and stand age in various ecosystem components: (a) aboveground vegetation, (b) woody tissues, (c) leaves, (d) litter, (e) the forest floor, and (f) mineral soil. The rate of absolute C change is determined as the slope of the relationship between C pool and stand age within each sequence. The x-axis shows the average age within each sequence. Two power functions are used to describe age-related soil C dynamics because of the opposite patterns occurring under C loss and accumulation scenarios. The open circles in panel (f) indicate soil C loss over age sequence (i.e. the rate of soil C pool change < 0), while the closed circles show soil C accumulation during stand development (i.e. the rate of soil C pool change > 0). The insets indicate the percentage of published studies showing various patterns of C dynamics over age sequence. Inc, increase; Dec, decrease; Not, no trend; Cov, Covington curve. Sample size (*n*) refers to the total number of analyzed sequences for each ecosystem component.

**Table 1** Pearson correlation coefficients between carbon dynamics in various ecosystem components and climatic variables across secondary forests around the world

Ecosystem component	MAT	MAP
Aboveground vegetation	0.33**	0.21*
Litter	0.31	0.10
Forest floor	0.70***	0.44**
Mineral soil	0.11	0.10

\*, *P* < 0.1; \*\*, *P* < 0.05; \*\*\*, *P* < 0.001.

MAT, mean annual temperature; MAP, mean annual precipitation.

*P* < 0.001), woody tissues ( $r^2 = 0.81$ , *P* < 0.05), leaves ( $r^2 = 0.89$ , *P* < 0.05), litter ( $r^2 = 0.61$ , *P* < 0.05), the forest floor ( $r^2 = 0.67$ , *P* < 0.05) and mineral soil ( $r^2 = 0.73$ , *P* < 0.001) during stand development (Fig. 4). The rate of relative N change was also positively associated with the rate

of relative C change in all ecosystem components (Fig. 5). However, the slope of the relationship between the rates of relative N and C changes was different among various ecosystem components (Fig. 5). The slope was < 1.0 in both aboveground vegetation (0.65) and woody tissues (0.67) (Fig. 5a–b), indicating slower rates of relative N change than relative C change in these two ecosystem components. By contrast, the slope was close to 1.0 in other ecosystem components (0.94 for leaves, 0.95 for litter, 1.00 for the forest floor and 0.90 for mineral soil) (Fig. 5c–f), showing similar rates of relative N and C changes in these ecosystem components.

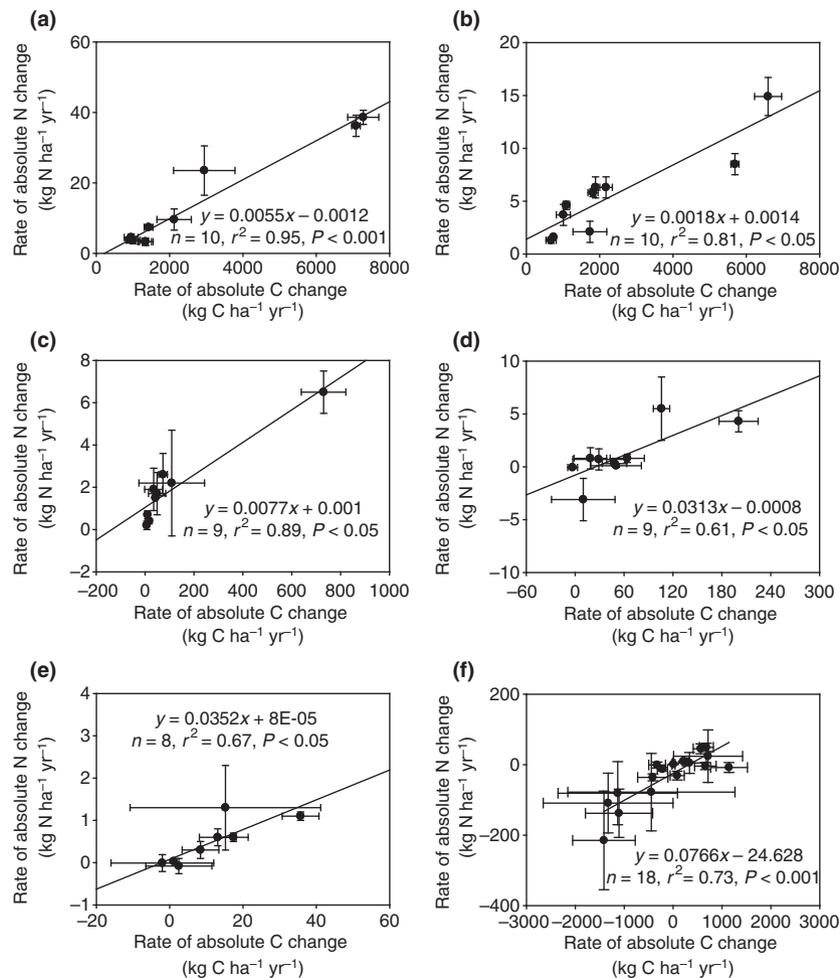
The increase of C pool size during stand development (Fig. 3) and the close associations between N and C changes (Figs 4–5) indicated that N also accumulated in forest ecosystems over age sequence. Similar to C pools, N pools in various ecosystem components exhibited different dominant

trends along the age gradient (Fig. 6). An increasing trend was the dominant pattern for N pools in aboveground vegetation, woody tissues, leaves, litter and the forest floor (Fig. 6a–e), whereas a statistically insignificant change was more common for the N pool in mineral soil (Fig. 6f). The associations between N and C changes (Figs 4–5) were also consistent with the changes in C : N ratios over age sequence (Fig. 7). As shown in Fig. 5, the rates of relative N changes were lower than the rates of relative C changes in both aboveground vegetation and woody tissues (Fig. 5a,b), while they were approximately equal in other ecosystem components (Fig. 5c–f). Accordingly, an increasing trend predominated for C : N ratios in both aboveground vegetation and woody tissues (Fig. 7a,b), while a statistically insignificant change was the most commonly observed pattern for C : N ratios in leaves, litter, the forest floor and mineral soil (Fig. 7c–f). Interestingly, the relative change in C : N ratio was > 1.0 in both aboveground vegetation (1.26) and woody tissues (1.32) (Fig. 7a,b), but close to 1.0 in other ecosystem com-

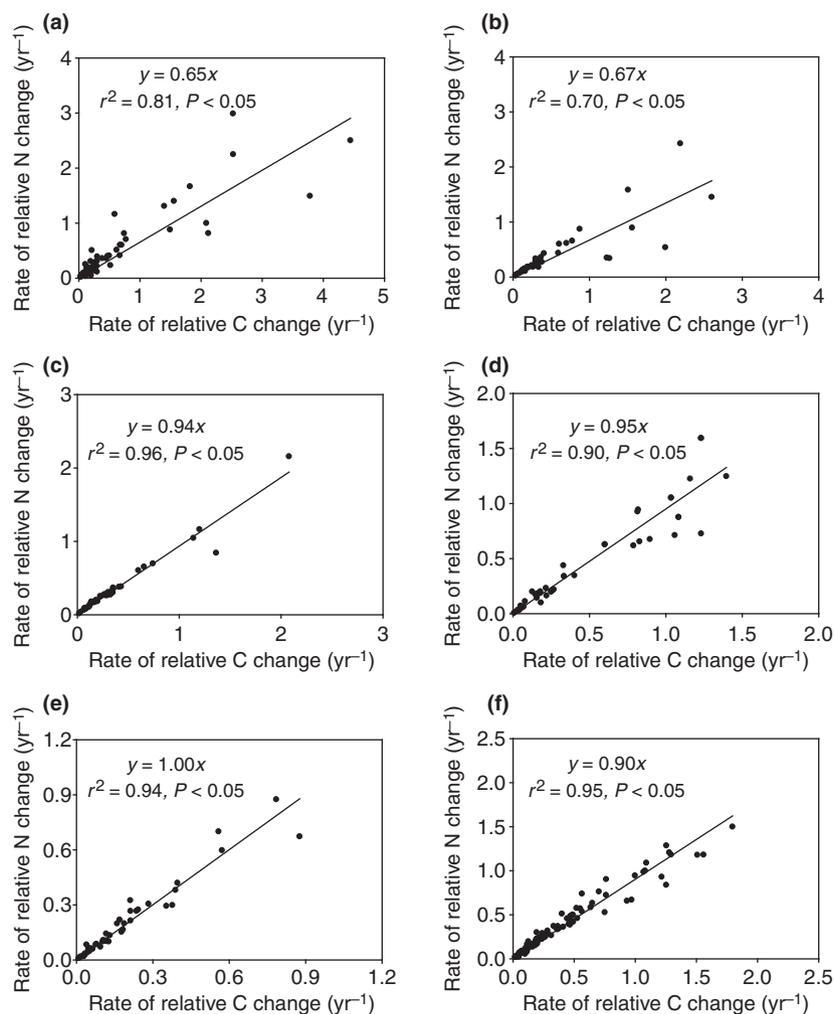
ponents (i.e. 1.05 for leaves, 1.05 for litter, 1.05 for the forest floor and 1.06 for mineral soil) (Fig. 7c–f). Thus, the relative change in C : N ratio also confirmed increasing C : N ratios in both aboveground vegetation and woody tissues but stable C : N ratios in other ecosystem components during stand development.

## Discussion

To our knowledge, this study provides the most comprehensive evaluation to date of C dynamics in both vegetation and soil during forest stand development. Our results show that vegetation C pools increased over age sequence. Similarly, C was found to accumulate in mineral soil in approximately one-fifth of the individual studies, but remained relatively stable in most cases along the age gradient. These results suggest that the C dynamics of mineral soils will not offset vegetation C sink during stand development. Our results also indicate that the rate of C pool changes declines with



**Fig. 4** Relationships between the rate of absolute nitrogen (N) change and the rate of absolute carbon (C) change in various ecosystem components: (a) aboveground vegetation, (b) woody tissues, (c) leaves, (d) litter, (e) the forest floor, and (f) mineral soil. The rate of absolute N change is expressed as the slope of the relationship between N pool and stand age within each sequence. The rate of absolute C change is determined in a similar manner. The error bars show the 95% confidence interval of the rates of absolute N and C changes.



**Fig. 5** Relationships between the rate of relative nitrogen (N) change and the rate of relative carbon (C) change in various ecosystem components: (a) aboveground vegetation, (b) woody tissues, (c) leaves, (d) litter, (e) the forest floor, and (f) mineral soil. The relative N change is defined as the N pool at the current age stage divided by the N pool at the previous age stage for each sequence. The rate of relative N change is determined as the relative change in N pool divided by the age interval between two adjacent age stages. The rate of relative C change is obtained in a similar manner.

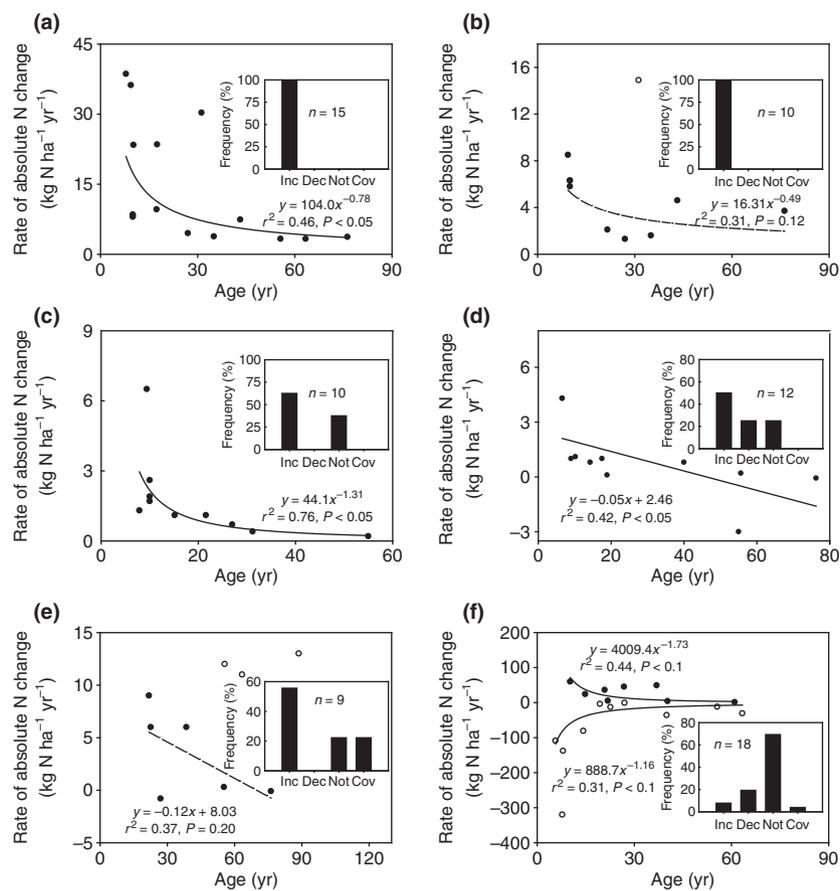
stand age and approaches an equilibrium state during the later stage of stand development, supporting Odum's succession theory (Odum, 1969). In addition, our results demonstrate that C accrual in forest ecosystems is accompanied by substantial N accretion over age sequence. The concurrent C and N dynamics suggest that forest ecosystems may have an intrinsic ability to accrue N and prevent progressive N limitation during long-term stand development. Taken together, the results obtained in this study provide a basis for evaluating the role of secondary forests in the global terrestrial ecosystem C cycle and understanding long-term C–N interactions in terrestrial ecosystems.

#### Ecosystem C dynamics during stand development

Vegetation C pools accrued over age sequence in most ecosystems. The accumulation of plant biomass along the age

gradient could be ascribed to the increase in leaf area index before canopy closure (Sprugel, 1984). It has frequently been observed that leaf area increases rapidly during the initial stage of stand development but approaches an asymptote or declines after canopy closure (Gower *et al.*, 1996). Accordingly, plant production is high during early stand development and then decreases with stand age (Ryan *et al.*, 1997). Thus, vegetation C pools usually show a relatively linear increase after disturbance followed by a saturation phase during the final stage of stand development (Odum, 1969). In addition, the increase in vegetation C pools over age sequence could also be driven by an increase in nutrient availability as a result of the increase in soil N mineralization following stand-replacing disturbances (White *et al.*, 2004; Davidson *et al.*, 2007).

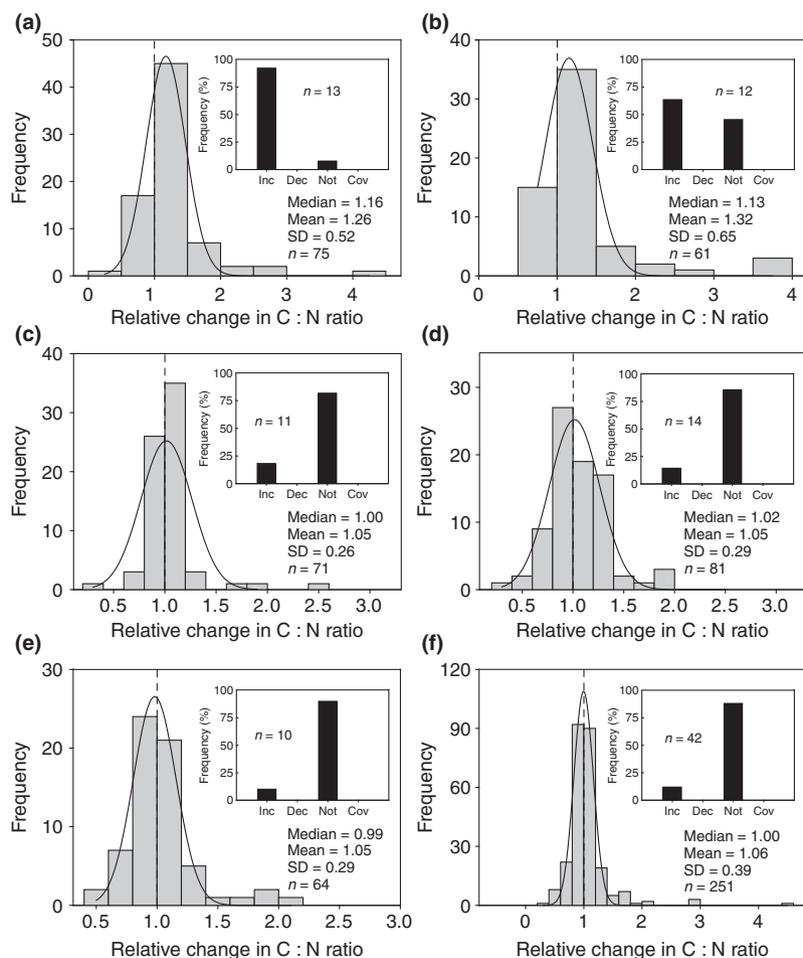
The soil C pool exhibited diverse dynamics during stand development, with a statistically insignificant change being



**Fig. 6** Relationships between the rate of absolute nitrogen (N) change and stand age in various ecosystem components: (a) aboveground vegetation, (b) woody tissues, (c) leaves, (d) litter, (e) the forest floor, and (f) mineral soil. The rate of absolute N change is expressed as the slope of the relationship between N pool and stand age within each sequence. The x-axis shows the average age within each sequence. The open circles in panels (b) and (e) indicate the outliers. Two power functions are used to describe age-related soil N dynamics because of the opposite patterns occurring under N loss and accumulation scenarios. The open circles in panel (f) represents soil N loss over age sequence (i.e. the rate of soil N pool change < 0), while the closed circles show soil N accumulation during stand development (i.e. the rate of soil N pool change > 0). The insets indicate the percentage of published studies showing various patterns of N dynamics over age sequence. Inc, increase; Dec, decrease; Not, no trend; Cov, Covington curve. Sample size ( $n$ ) refers to the total number of analyzed sequences for each ecosystem component.

predominant. The diverse patterns of soil C dynamics may be related to the specific type of disturbance before forest establishment. To test this possibility, we summarized the age-related dynamics in soil C pool according to the disturbance type (i.e. fire, harvest, agricultural abandonment or plantation). Our results showed that agricultural abandonment made a major contribution to the increase in soil C pool over age sequence, while plantation was responsible for a decline in soil C pool during stand development (Fig. S1). It is well known that the changes in soil C stock driven by disturbance are largely determined by changes in the input rates of organic matter and its decomposability (Post & Kwon, 2000). The forest that becomes established after agricultural abandonment usually consists of highly productive tree species with low litter quality and thus is favourable for C accumulation in mineral soil (Don *et al.*, 2010). By contrast, plantation deposits more C as litter to the forest floor,

which is incorporated more slowly into mineral soil than in native ecosystems, leading to C loss from mineral soil (Berthrong *et al.*, 2009). Nevertheless, our results indicated that a statistically insignificant change dominated under all disturbance types (Fig. S1), suggesting that the dominant pattern of soil C dynamics was independent of disturbance type. The insignificant C dynamics of mineral soil may result from a dynamic balance between C input from plant production and output through microbial decomposition (Davidson & Janssens, 2006). During stand development, C accumulated in both litter and the forest floor in most cases (Fig. 3d,e). The increase in C pools in both litter and the forest floor could lead to more C inputs into mineral soil through subsequent dissolved organic C leaching or mixing by microfauna (Chapin *et al.*, 2002). However, microbial decomposition was frequently observed to accelerate after a stand-replacing disturbance (Covington, 1981; Zak *et al.*,



**Fig. 7** Frequency distributions of the relative changes in carbon : nitrogen (C : N) ratios in various ecosystem components: (a) aboveground vegetation, (b) wood, (c) leaves, (d) litter, (e) the forest floor, and (f) mineral soil. The relative change in the C : N ratio is defined as the C : N ratio at the current age stage divided by the C : N ratio at the previous age stage for each sequence. The dashed line shows that the relative change in the C : N ratio is equal to 1.0, indicating that the C : N ratio is constant over the two adjacent age stages. The inserts represent the percentage of published studies showing various patterns of C : N ratio dynamics over age sequence. Inc, increase; Dec, decrease; Not, no trend; Cov, Covington curve. Sample size ( $n$ ) refers to the total number of analyzed sequences for each ecosystem component.

1990). As a consequence, the enhanced C input from litter and the forest floor may be balanced by the increased C output driven by microbial decomposition and thus result in a relatively stable soil C pool over age sequence.

Potential uncertainties may be introduced into the overall pattern of soil C dynamics observed in this study, as soil C pools at the original depth were converted to a depth of 1 m using the depth functions developed by Jobbágy & Jackson (2000). To evaluate such uncertainties, we examined changes in soil C pool at the original depth for each individual study and then re-summarized the overall pattern. Our results confirmed that soil C stock did not exhibit significant changes with stand age in most studies (Fig. S2), consistent with results having depth corrections (Fig. 3). These consistencies suggest that depth corrections do not alter the overall pattern of soil C dynamics during stand development. Nevertheless, the potential changes in root distributions, dissolved organic C and organic matter turnover over age

sequence may result in some uncertainties in soil C corrections calculated using fixed depth functions. Unfortunately, there is little experimental evidence showing that root distributions may exhibit significant changes during forest stand development. To the best of our knowledge, only one study examined changes in vertical distributions of roots along the age gradient, and revealed that the changes in root distributions over age sequence were not statistically significant (Yanai *et al.*, 2006). Similarly, changes in dissolved organic C with stand age remain equivocal (e.g. Peichl *et al.*, 2007; Teklay & Chang, 2008). Thus, to gain more insight into the potential uncertainties involved in depth corrections, more individual studies should be conducted to examine changes in the vertical distributions of roots, dissolved organic C and organic matter turnover rate over age sequence. More directly, a number of actual observations are required to evaluate changes in the vertical distributions of the soil C pool during forest stand development. In addition, more frequent

measurements at different developmental stages are needed to produce a realistic picture of soil C dynamics along the age gradient.

### Effects of biophysical factors on forest C dynamics

The rates of C pool changes in both vegetation and soil declined markedly with stand age, and C dynamics in all ecosystem components tended to reach equilibrium during the latter stage of stand development, indicating that stand age plays a discernible role in shaping the trajectory of C dynamics across secondary forests around the world (Pregitzer & Euskirchen, 2004). These results accord well with Odum's succession theory, which predicts that C dynamics tend to be balanced during the later stage of ecosystem development (Odum, 1969). These results are also consistent with a recent 'dynamic disequilibrium' framework, which states that disturbance leads to temporal changes in ecosystem C pool within one disturbance–recovery episode but does not affect long-term C dynamics unless the disturbance regime changes (Luo & Weng, 2010). The decreased rate of C pool change with stand age could be largely driven by the decline of vegetation net primary production (NPP) during stand development (Ryan *et al.*, 1997, 2009). The decrease of C accumulation rate over age sequence may also be attributable to an upper limit on the amount of C that can be stored per unit land area (Silver *et al.*, 2000). The decreased rate of C pool change with stand age should be incorporated into land surface models when projecting future terrestrial C dynamics under global change scenarios (Zaehle *et al.*, 2006).

The rate of C pool changes in both vegetation and forest floor increased with MAT and MAP, while that in mineral soil did not vary with either MAT or MAP. The increased rate of vegetation C pool change along the climatic gradient is consistent with the fact that tropical forests usually grow more rapidly than temperate and boreal forests (Bonan, 2008). Such a pattern may be induced by the stimulating effects of temperature and moisture on vegetation growth (Luyssaert *et al.*, 2007). The different relationships of the rates of C pool changes in the forest floor and mineral soil with climatic factors were indirectly indicated by the different associations of the rates of C pool changes in the forest floor and mineral soil with the rate of C pool change in aboveground vegetation (Fig. S3). Specifically, the rate of C pool changes in the forest floor was closely correlated with that in aboveground vegetation ( $r = 0.65$ ,  $P < 0.05$ ) (Fig. S3a), while the rate of C pool changes in mineral soil did not show any significant association with that in aboveground vegetation ( $r = -0.11$ ,  $P = 0.64$ ) (Fig. S3b). As a consequence, the increased rate of C pool changes in the forest floor along the climatic gradient may be indirectly driven by their stimulating effects on vegetation C accumulation during stand development. However, the weak relationships

between the rate of soil C pool changes and climatic factors presumably stem from similar effects of climatic variables on vegetation production and microbial decomposition. It is well established that both vegetation growth (Luyssaert *et al.*, 2007) and microbial activity (Raich & Schlesinger, 1992) tend to be faster and higher under warmer/wetter conditions than under colder/drier conditions. Thus, the similar effects of climatic factors on C inputs and outputs to mineral soil could lead to the weak associations between the rate of soil C pool changes and climatic variables.

### N accrual and its implications for long-term C accumulation

The accumulation of C stock during long-term stand development was accompanied by N accretion in vegetation, litter and the forest floor (Figs 4–6). To quantify changes in N pools during forest stand development, we estimated the rate of N accumulation over age sequence for each ecosystem component. First, N accretion in aboveground vegetation was estimated to be  $8.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , using the median value of 15 age sequences. Because of the lack of root N information in the literature, the rate of N accumulation in belowground vegetation over age sequence was estimated using data on N accretion in aboveground vegetation and root : shoot ratio in forest ecosystems. Assuming that the root : shoot ratio in forest ecosystems is 0.3 (Mokany *et al.*, 2006), the rate of N accumulation in belowground vegetation was roughly equal to  $2.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . Similarly, litter and the forest floor could accumulate N at rates of 1.0 and  $11.0 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , respectively, during stand development. In total, the accrual of ecosystem N capital over age sequence was estimated to be  $22.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , within the range of 0– $120 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  reported by Binkley *et al.* (2000). Where does the additional N come from? The increases in N pools in vegetation, litter and the forest floor could be largely derived from the external inputs from atmospheric N deposition and biological N fixation (Bormann *et al.*, 1993; Davidson *et al.*, 2007). The increased N pools in vegetation, litter and the forest floor could also come from deeper soil as a result of an increase in root exploration of soil for available N, such as increasing biomass allocation to fine roots (Iversen *et al.*, 2010). In addition, the soil N availability stimulated by the rhizospheric interactions between plants and microbes could be an important source of N supporting forest production across decades and centuries. It has been reported that increased soil organic matter decomposition as a result of the priming effects of rhizosphere microbes may contribute a large proportion of available N in mineral soil (Phillips, 2007; Frank & Groffman, 2009).

The increases in ecosystem N capital revealed in this study have important implications for long-term C sequestration in terrestrial ecosystems. It is well known that

additional N is required to support terrestrial C accumulation as a result of stoichiometric relationships in both vegetation and soil (Hungate *et al.*, 2003). If ecosystems cannot capture enough N to match the increases in C storage, the terrestrial C sink will be down-regulated and will not be sustained in the long term (Hungate *et al.*, 2003; Luo *et al.*, 2004; Reich *et al.*, 2006). However, ecosystems have a number of processes to mitigate the degree of N regulation of C sequestration. Over short and intermediate time scales, either an increase in the C : N ratio or N redistribution from mineral soil with low C : N ratio to vegetation with high C : N ratio can increase the capability of terrestrial ecosystems to sequester C without additional N inputs (Rastetter *et al.*, 1997; Luo *et al.*, 2004). By contrast, a long-term sustainable terrestrial C sink requires an increase in ecosystem N capital (Rastetter *et al.*, 1997; Luo *et al.*, 2004). Our results showed substantial N accretion in various ecosystem components, demonstrating that natural ecosystems may have an intrinsic ability to accrue N for additional C accumulation along the age gradient. Subsequently, the increased ecosystem N capital may promote internal N cycling through enhanced N mineralization (Schimel *et al.*, 1997; Davidson *et al.*, 2007) and enable mineral soils to provide more available N to support forest growth (Rastetter *et al.*, 1997; Davidson *et al.*, 2007). Therefore, N accretion in forest ecosystems may preclude progressive N limitation over age sequence (Luo *et al.*, 2006a) and will be favorable for maintaining forest C accumulation during long-term stand development (Knops & Tilman, 2000).

## Acknowledgements

We are grateful to Dr Amy Austin and four anonymous reviewers for their insightful comments which greatly improved the manuscript. We also thank Dr Rebecca Sherry and Mr Joshua Kalfas for assisting with English grammar. We thank all the scientists whose data and work were included in this data synthesis. This study was financially supported by the US National Science Foundation (NSF) (grants DEB 0743778, DEB 0840964, DBI 0850290 and EPS 0919466); by the Office of Science (BER), Department of Energy (grant DE-FG02-006ER64319); and by the Midwestern Regional Center of the National Institute for Climatic Change Research at Michigan Technological University (grant DE-FC02-06ER64158).

## References

- Bellamy PH, Loveland PJ, Bradley RI, Lark RM, Kirk GJD. 2005. Carbon losses from all soils across England and Wales 1978–2003. *Nature* 437: 245–248.
- Berthrong ST, Jobbágy EG, Jackson RB. 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecological Applications* 19: 2228–2241.
- Binkley D, Son Y, Valentine DW. 2000. Do forests receive occult inputs of nitrogen? *Ecosystems* 3: 321–331.
- Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.
- Bormann BT, Bormann FH, Bowden WB, Pierce RS, Hamburg SP, Wang D, Snyder M, Li CY, Ingersoll R. 1993. Rapid N<sub>2</sub> fixation in pines, alder, and locust: evidence from the sandbox ecosystem study. *Ecology* 74: 583–598.
- Carpenter SR, Armbrust V, Arzberger P, Chapin F III, Elser J, Hackett E, Ives A, Kareiva P, Leibold M, Peters DC. 2009. Accelerate synthesis in ecology and environmental sciences. *BioScience* 59: 699–701.
- Chapin FS III, Matson PA, Mooney HA. 2002. *Principles of terrestrial ecosystem ecology*. New York, NY, USA: Springer.
- Covington WW. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* 62: 41–48.
- Davidson EA, de Carvalho CJ, Figueira AM, Ishida FY, Ometto JP, Nardoto GB, Sabá RT, Hayashi SN, Leal EC, Vieira IC. 2007. Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447: 995–998.
- Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440: 165–173.
- Don A, Schumacher J, Freibauer A. 2010. Impact of tropical land-use change on soil organic carbon stocks – a meta-analysis. *Global Change Biology*. doi: 10.1111/j.1365-2486.2010.02336.x.
- Finzi AC, Allen AS, DeLucia EH, Ellsworth DS, Schlesinger WH. 2001. Forest litter production, chemistry, and decomposition following two years of free-air CO<sub>2</sub> enrichment. *Ecology* 82: 470–484.
- Finzi AC, Moore DJP, DeLucia EH, Lichten J, Hofmockel KS, Jackson RB, Kim H-S, Matamala R, McCarthy HR, Oren R. 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO<sub>2</sub> in a warm-temperate forest. *Ecology* 87: 15–25.
- Frank DA, Groffman PM. 2009. Plant rhizospheric N processes: what we don't know and why we should care. *Ecology* 90: 1512–1519.
- Gough CM, Vogel CS, Harrold KH, George K, Curtis PS. 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. *Global Change Biology* 13: 1935–1949.
- Gower ST, McMurtrie RE, Murty D. 1996. Aboveground net primary production decline with stand age: potential causes. *Trends in Ecology and Evolution* 11: 378–382.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- Houghton RA, Hall F, Goetz SJ. 2009. Importance of biomass in the global carbon cycle. *Journal of Geophysical Research* 114: G00E03, doi: 10.1029/2009JG000935.
- Hungate BA, Dukes JS, Shaw MR, Luo YQ, Field CB. 2003. Nitrogen and climate change. *Science* 302: 1512–1513.
- Hungate BA, Stiling PD, Dijkstra P, Johnson DW, Ketterer ME, Hymus GJ, Hinkle CR, Drake BG. 2006. Nitrogen cycling during seven years of atmospheric CO<sub>2</sub> enrichment in a scrub oak woodland. *Ecology* 87: 26–40.
- Iversen CM, Hooker TD, Classen AT, Norby RJ. 2010. Net mineralization of N at deeper soil depths as a potential mechanism for sustained forest production under elevated [CO<sub>2</sub>]. *Global Change Biology* 17: 1130–1139.
- Jobbágy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10: 423–436.
- Jobbágy EG, Jackson RB. 2001. The distribution of soil nutrients with depth: global patterns and the imprint of plants. *Biogeochemistry* 53: 51–77.

- Johnson CM, Zarin DJ, Johnson AH. 2000. Post-disturbance aboveground biomass accumulation in global secondary forests. *Ecology* 81: 1395–1401.
- Johnson DW. 2006. Progressive N limitation in forests: review and implications for long-term responses to elevated CO<sub>2</sub>. *Ecology* 87: 64–75.
- Kauppi PE, Ausubel JH, Fang JY, Mather AS, Sedjo RA, Waggoner PE. 2006. Returning forests analyzed with the forest identity. *Proceedings of the National Academy of Sciences, USA* 103: 17574–17579.
- Knops JM, Tilman D. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81: 88–98.
- Law BE, Thornton PE, Irvine J, Anthoni PM, Tuyl SV. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology* 7: 755–777.
- Lu M, Yang YH, Luo Y, Fang CM, Zhou XH, Chen JK, Yang X, Li B. 2010. Responses of ecosystem nitrogen cycle to nitrogen addition: a meta-analysis. *New Phytologist* 189: 1040–1050.
- Luo YQ, Field CB, Jackson RB. 2006a. Do nitrogen constrain carbon cycling, or does carbon input stimulate nitrogen cycling? *Ecology* 87: 3–4.
- Luo YQ, Hui DF, Zhang DQ. 2006b. Elevated CO<sub>2</sub> stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology* 87: 53–63.
- Luo YQ, Su B, Currie WS, Dukes JS, Finzi A, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ *et al.* 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54: 731–739.
- Luo YQ, Weng ES. 2010. Dynamic disequilibrium of the terrestrial carbon cycle under global change. *Trends in Ecology and Evolution* 2: 96–104.
- Luyssaert S, Inglis I, Jung M, Richardson AD, Reichstein M, Papale D, Piao SL, Schulze E-D, Wingate L, Matteucci G *et al.* 2007. CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology* 13: 2509–2537.
- Luyssaert S, Schulze E-D, Börner A, Knohl A, Hessenmöller D, Law BE, Ciais P, Grace J. 2008. Old-growth forests as global carbon sinks. *Nature* 455: 213–215.
- Mokany K, Raison RJ, Prokushkin AS. 2006. Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology* 11: 1–13.
- Norby RJ, Iversen CM. 2006. Nitrogen uptake, distribution, turnover, and efficiency of use in a CO<sub>2</sub>-enriched sweetgum forest. *Ecology* 87: 5–14.
- Odum EP. 1969. The strategy of ecosystem development. *Science* 164: 262–270.
- O'Neill KP, Richter DD, Kasischke ES. 2006. Succession-driven changes in soil respiration following fire in black spruce stands of interior Alaska. *Biogeochemistry* 80: 1–20.
- Peichl M, Moore TR, Arain MA, Dalva M, Brodkey D, McLaren J. 2007. Concentrations and fluxes of dissolved organic carbon in an age-sequence of white pine forests in Southern Ontario, Canada. *Biogeochemistry* 86: 1–17.
- Peltoniemi M, Makipaa R, Liski J, Tamminen P. 2004. Changes in soil carbon with stand age – an evaluation of a modeling method with empirical data. *Global Change Biology* 10: 2078–2091.
- Perez CA, Carmona MR, Aravena JC, Armesto JJ. 2004. Successional changes in soil nitrogen availability, non-symbiotic nitrogen fixation and carbon/nitrogen ratios in southern Chilean forest ecosystems. *Oecologia* 140: 617–625.
- Phillips RP. 2007. Towards a rhizo-centric view of plant–microbial feedbacks under elevated atmospheric CO<sub>2</sub>. *New Phytologist* 173: 664–667.
- Post WM, Kwon KC. 2000. Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology* 6: 317–327.
- Pregitzer KS, Euskirchen ES. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology* 10: 2052–2077.
- R Development Core Team. 2007. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raich JW, Schlesinger WH. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus (Series B)* 44: 81–99.
- Rastetter EB, Agren GI, Shaver GR. 1997. Responses of N-limited ecosystems to increased CO<sub>2</sub>: a balanced-nutrition, coupled-element-cycle model. *Ecological Applications* 7: 444–460.
- Reich PB, Hungate BA, Luo YQ. 2006. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution, and Systematics* 37: 611–636.
- Rothstein DE, Yermakov Z, Buell AL. 2004. Loss and recovery of ecosystem carbon pools following stand-replacing wildfire in Michigan jack pine forests. *Canadian Journal of Forest Research* 34: 1908–1918.
- Running SW. 2008. Ecosystem disturbance, carbon, and climate. *Science* 321: 652–653.
- Ryan MG, Binkley D, Fownes JH. 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* 27: 213–262.
- Ryan MG, Cavaleri MA, Almeida AC, Penchel R, Senock RS, Stape JL. 2009. Wood CO<sub>2</sub> efflux and foliar respiration for *Eucalyptus* in Hawaii and Brazil. *Tree Physiology* 29: 1213–1222.
- Schimmel DS, Braswell BH, Parton WJ. 1997. Equilibration of the terrestrial water, nitrogen, and carbon cycles. *Proceedings of the National Academy of Sciences, USA* 94: 8280–8283.
- Silver WL, Ostertag R, Lugo AE. 2000. The potential for carbon sequestration through reforestation of abandoned agricultural and pasture lands. *Restoration Ecology* 4: 394–407.
- Sprugel DG. 1984. Density, biomass, productivity, and nutrient-cycling changes during stand development in Wave-regenerated Balsam Fir forests. *Ecological Monographs* 54: 165–186.
- Strain BR, Bazzaz FA. 1983. Terrestrial plant communities. In: Lemon ER, ed. *CO<sub>2</sub> and Plants. American Association for the Advancement of Science selected symposium*. Boulder, CO, USA: Westview Press, 177–222.
- Teklay T, Chang SX. 2008. Temporal changes in soil carbon and nitrogen storage in a hybrid poplar chronosequence in northern Alberta. *Geoderma* 144: 613–619.
- White LL, Zak DR, Barnes BV. 2004. Biomass accumulation and soil nitrogen availability in an 87-yr-old *Populus grandidentata* chronosequence. *Forest Ecology and Management* 191: 121–127.
- Yanai RD, Park BB, Hamburg SP. 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. *Canadian Journal of Forest Research* 36: 450–459.
- Zaehle S, Sitch S, Prentice IC, Liski J, Cramer W, Erhard M, Hickler T, Smith B. 2006. The importance of age-related decline in forest NPP for modeling regional carbon balances. *Ecological Applications* 16: 1555–1574.
- Zak DR, Grigal DF, Gleeson S, Tilman D. 1990. Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. *Biogeochemistry* 11: 111–129.
- Zhou G, Liu S, Li Z, Zhang D, Tang X, Zhou C, Yan J, Mo J. 2006. Old-growth forests can accumulate carbon in soils. *Science* 314: 1417.

## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Frequency distribution of published studies showing various patterns of soil carbon (C) dynamics under various disturbance types.

**Fig. S2** Frequency distribution of published studies showing various patterns of soil carbon (C) dynamics over age sequence, generated using soil C data at the original soil depth.

**Fig. S3** Relationships between the rate of carbon (C) change in the forest floor and the rate of C change in aboveground vegetation (a) and between the rate of C change in mineral soil and the rate of C change in aboveground vegetation (b) during stand development.

**Table S1** Characteristics of 124 age sequences included in this study

**Notes S1** A list of papers from which data are extracted for this study.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.