New Phytologist

Global patterns of the dynamics of soil carbon and nitrogen stocks following afforestation: a meta-analysis

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Received: *21 January 2012*
Accepted: *12 March 2012*

New Phytologist (2012) **195**: 172–181
doi: 10.1111/j.1469-8137.2012.04150.x

Key words: afforestation, carbon–nitrogen interaction, dynamics, global pattern, meta-analysis, soil nitrogen, soil organic carbon.

Summary

- Afforestation has been proposed as an effective method of carbon (C) sequestration; however, the magnitude and direction of soil carbon accumulation following afforestation and its regulation by soil nitrogen (N) dynamics are still not well understood.
- We synthesized the results from 292 sites and carried out a meta-analysis to evaluate the dynamics of soil C and N stocks following afforestation.
- Changes in soil C and N stocks were significantly correlated and had a similar temporal pattern. Significant C and N stock increases were found 30 and 50 yr after afforestation, respectively. Before these time points, C and N stocks were either depleted or unchanged. Carbon stock increased following afforestation on cropland and pasture, and in tropical, subtropical and boreal zones. The soil N stock increased in the subtropical zone. The soil C stock increased after afforestation with hardwoods such as Eucalyptus, but did not change after afforestation with softwoods such as pine. Soil N stocks increased and decreased, respectively, after afforestation with hardwoods (excluding Eucalyptus) and pine.
- These results indicate that soil C and N stocks both increase with time after afforestation, and that C sequestration through afforestation depends on prior land use, climate and the tree species planted.

Introduction

Carbon (C) stored in forest ecosystems represents a substantial part of the global C budget. It is estimated that forest standing biomass accounts for 82–86% of above-ground C content and forest soils contain 70–73% of the global soil organic C (soil C hereafter) (Six *et al.*, 2002). Following cultivation of previously forested lands (deforestation), soil C can be rapidly lost as a result of enhanced C decomposition and erosion caused by soil disturbance (Lal, 2005). It was reported that up to 50% of soil C was lost within the first 20 yr (Lal, 2005). Forest plantation, either afforestation or reforestation, on the other hand, has been suggested to reverse the process of deforestation and may bring about accumulation of C (Metz *et al.*, 2007). For this reason, afforestation and reforestation were proposed as an effective method of C sequestration in Article 3.3 of the Kyoto Protocol.

However, the effects of afforestation on soil C accumulation and the related influencing factors are not well understood. According to the results of individual studies, afforestation either increased (Resh *et al.*, 2002; Lemma *et al.*, 2006; Hernandez-Ramirez *et al.*, 2011) or decreased (Farley *et al.*, 2004; Zhao *et al.*, 2007; Mao & Zeng, 2010) soil C accumulation. Other studies found a negligible change in soil C pool after afforestation. For example, Richter *et al.* (1999) reported that, despite high C inputs to the mineral soil, C sequestration was quite limited (< 1% of total ecosystem C accumulation) relative to trees (*c.* 80%) and the forest floor (*c.* 20%). The inconsistent conclusions from the individual studies likely arise because the magnitude and direction of soil C dynamics are affected by multiple factors, including climate, soil type, tree species planted and nutrient management (Paul *et al.*, 2002; Lal, 2004; Laganière *et al.*, 2010). It will undoubtedly be helpful to determine the general patterns and the major controlling factors of soil C accumulation in order to provide support for policy-making in relation to C sequestration via afforestation.

Several quantitative reviews have been published that are relevant to C stock dynamics following afforestation (Post & Kwon, 2000; Guo & Gifford, 2002; Paul *et al.*, 2002; Berthrong *et al.*, 2009; Laganière *et al.*, 2010). However, the results of these studies are inconsistent, possibly because of the methods of handle sampling depths. It is well documented that soil C stock changes after afforestation vary with depth (Paul *et al.*, 2002; Don *et al.*, 2011), but most reviews did not consider the sampling depths well in their analysis (Guo & Gifford, 2002; Berthrong *et al.*, 2009; Laganière *et al.*, 2010; Don *et al.*, 2011). Another reason for the inconsistency could be the method of handling the organic layer of the soil profile; this was included in some reviews but was combined with the mineral layer for data analysis, although data from the organic layer were quite limited (Laganière *et al.*, 2010).

Furthermore, the existing quantitative reviews only focused on soil C accumulation, neglecting soil nitrogen (N) dynamics and

C–N interactions, which are very important in determining whether the C sink in land ecosystems could be sustained over the long term (Luo *et al.*, 2004, 2006a; Finzi *et al.*, 2006). It has been suggested that N dynamics is a key parameter in the regulation of long-term terrestrial C sequestration (Rastetter *et al.*, 1997; Luo *et al.*, 2004). The modeling studies demonstrated that N capital in an ecosystem determines the long-term trend of the terrestrial C sink, which will be sustained only when there is increased N input into an ecosystem (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 does 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 N availability or decreased N losses, progressive N limitation will not occur (Luo *et al.*, 2006a). Therefore, it is imperative to quantify N capital changes and to analyze relationships between C and N stock dynamics following afforestation.

In this paper, a meta-analysis was carried out to study the dynamics of both soil C and N stocks. Data from organic and mineral layers were extracted from the published papers and standardized to improve the comparison. The major questions we aimed to answer were as follows: how do C and N stocks change following afforestation; how do prior land use, climate and tree species planted affect C and N dynamics following afforestation; and how does the change in N stock change correlate with the change in C stock?

Materials and Methods

Data compilation

The following criteria were used to select the papers: soil C stock, N stock or both were presented or could be calculated based on percentage contents of C and N, bulk density and sampling depth; there were data for both the afforested sites (LU2) and the prior land use sites (LU1); the experiments used paired-site, chronosequence, or retrospective design, with similar soil conditions for both LU2 and LU1; years since afforestation were either clearly pointed out or could be directly derived; studies reporting short-term effects (< 5 yr) were excluded; only afforestation of the first rotation was considered; and data for both the organic and mineral layers of the soil profile were extracted. In addition, studies were rejected for the data compilation if they were subject to a lack of replications or if the paired sites or sites of chronosequence were confounded by different soil types. In total, the dataset included 292 sites reported by 70 peer-reviewed papers, of which 58 reported mineral layer data and 33 reported organic layer data (Supporting information, Table S1 and Notes S1).

The raw data were either obtained from tables or extracted by digitizing graphs using the GetData Graph Digitizer (version 2.24, Russian Federation). For each paper, the following information was compiled: sources of data, location (country, longitude and latitude), climatic information (climate zone, mean annual temperature and mean annual precipitation), land use type before afforestation (cropland, pasture and natural grassland), tree species planted (Eucalyptus, hardwoods (excluding Eucalyptus), pine, and softwoods (excluding pine)), years since afforestation (or plantation age), sampling depth, experimental design (paired site, chronosequence, retrospecitve design), soil size, soil texture (classification, clay content, pH), and amount of soil C and N in mineral and organic layers. In studies that sampled many replicate plots over a landscape, those plots with the same age, edaphic conditions, and land use were pooled. When more than one depth was sampled, C and N stocks at all the depths were summed together. Where a particular chronosequence or retrospective study had observations at a number of plantation ages, each age was regarded as an independent study and included in the analysis. The final dataset was separated into two subsets, that is, one for the mineral layer and another for the organic layer, as not all studies considered both layers and this separation would therefore reduce uncertainty. The ages of afforestation were divided into six groups, as follows: 5–10, 10–20, 20–30, 30–40, 40–50 and ≥ 50 yr. Prior land use types were grouped into cropland, natural grassland, and pasture. Climate zones were classified into five zones – boreal, temperate continental, temperate maritime, subtropical and tropical – based on Köppen's classification (Laganière *et al.*, 2010). Tree species planted were categorized into pine, Eucalyptus, hardwoods (excluding Eucalyptus), and softwoods (excluding pine).

When data in the original papers were presented as percentage concentration, C or N stock (g m^{-2}) was calculated based on the percentage concentration of C or N, bulk density and sampling depth (Guo & Gifford, 2002). Although it is desirable to compare changes in soil C or N stocks between land uses based on common soil mass rather than on volume because of compaction, it is impossible for us to correct data for all these studies, as not all the studies reported bulk densities, especially bulk densities for different soil depths. Thus, similar to other meta-analyses (Guo & Gifford, 2002; Laganière *et al.*, 2010; Powers *et al.*, 2011), we did not adjust reported data to a common mass, but we used mass-corrected soil C and N stocks when authors presented them. Not adjusting for an equivalent mass of soil could only result in a slight bias in the estimation of changes in soil C and N stocks, which is supported by our data (Fig. S1) and also by other studies (Laganière *et al.*, 2010).

To increase the comparability of data derived from different studies, the methodology adopted by Yang *et al.* (2011) was used in the present study. The original soil C or N data were converted to the soil C or N stocks in the top 100 cm using the depth functions developed by Jobbágy & Jackson (2000, 2001) according to the following equations:

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

$$X_{100} = \frac{1 - \beta^{100}}{1 - \beta^{d0}} \times X_{d0} \qquad \text{Eqn 2}$$

where Y represents the cumulative proportion of the soil C (or N) stock from the soil surface to depth d (cm); β is the relative rate of decrease in the soil C (or N) stock with soil depth; X_{100} denotes the soil C (or N) stock in the upper 100 cm (g m^{-2}); d_0 denotes the original soil depth available in individual studies (cm); and X_{d0} is the original soil C (or N) stock (g m^{-2}). For soil N, only the global averaged depth distribution was provided in Jobbágy & Jackson (2001). For soil C, although Jobbágy & Jackson (2000) provided the depth distributions for 11 biome types globally, there was no significant difference ($P > 0.98$, ANOVA LSD test using PASW 18 (SPSS Inc., Chicago, IL, USA)) in the depth distribution among biome types or between individual biomes and the global average. Therefore, in this study, the global average depth distributions for both C and N were adopted to calculate the value of β (0.9786 for C and 0.9831 for N) in Eqn 1.

It should be noted that potential uncertainties may be introduced by this dataset standardization, mainly as a result of the difference in C and N distribution over the soil profile between prior land use types and afforested sites, and among different stages of forest development. However, as has been stated, there was no significant difference among the 11 biome types included in Jobbágy & Jackson (2000) or between individual biomes and the global average in terms of the soil C distribution with depth. The same method (i.e. converting the original C and N stocks to the stocks in the top 100 cm using the depth functions in order to increase comparability) was used by Yang *et al.* (2011), and it was concluded that depth correction did not alter the overall pattern of soil C and N stock dynamics during stand development. Our data show that the measured and calculated stocks to a depth of 100 cm for both C and N fit very well, and there is no difference between the measured and calculated values for C stocks, but this method could overestimate N stocks by up to 29% (Fig. S2).

Data calculation and analysis

All studies have measurements that represent changes in soil C or N stock during at least one time interval, which makes it possible to calculate the rate of absolute stock change by dividing the total C or N stock change by the time since afforestation (yr) (Eqn 3), although these rates may not be constant over the time interval:

$$\text{Rate of absolute stock change}\,(\mathrm{g\ m^{-2}yr^{-1}}) = \frac{\Delta X}{\Delta t} \qquad \text{Eqn 3}$$

where ΔX denotes the variation of soil C (or N) stocks following afforestation, and Δt represents time since afforestation (yr). In addition, in order to reflect the rate change of C relative to N, or vice versa, rates of relative stock change were calculated according to Eqn 4:

$$\text{Rate of relative stock change}\,(\%\ \mathrm{yr^{-1}}) = \frac{\Delta X}{X_{\mathrm{LU1}} \times \Delta t} \times 100\% \qquad \text{Eqn 4}$$

where X_{LU1} represents C or N stocks before afforestation (retrospective design) or estimated from an adjacent control site (paired site or chronosequence). As C or N stocks in the organic layer were sometimes zero for LU1, especially for cropland, the rate of relative stock change was not calculated for the organic layer.

The 95% confidence interval (CI) was calculated for the overall data and for each category. In order to reflect the dynamics of total soil C or N stocks, the mean rates of absolute stock change for mineral and organic layers were summed for each category. In this case, a methodology reported previously (Luo *et al.*, 2006b, 2009) was used to calculate 95% CI of means for total C or N, as shown in Eqns 5 and 6:

$$\mathrm{SE_{total}} = \sqrt{\frac{V_{\mathrm{organic}}}{n_1} + \frac{V_{\mathrm{mineral}}}{n_2}} \qquad \text{Eqn 5}$$

$$95\%\ \mathrm{CI} = 1.96 \times \mathrm{SE_{total}} \qquad \text{Eqn 6}$$

where $\mathrm{SE_{total}}$ denotes the standard error of the mean for rates of absolute stock change for total C or N; V_{organic} and n_1 are the variance of stock change rates and the number of observations, respectively, for the organic layer; and V_{mineral} and n_2 are the variance of stock change rates and the number of observations, respectively, for the mineral layer. In this study, the observed effect sizes are considered statistically different from zero if the 95% CI does not include zero, and the grouping factors are considered significantly different from each other if their 95% CI does not overlap.

In order to evaluate C–N interactions following afforestation, a regression analysis was conducted to analyze the relationship between rates of absolute C stock change and absolute N stock change and between rates of relative C change and relative N change for the mineral layer. The regression analysis and figures were performed using SigmaPlot 10.0 (Systat, San Jose, CA, USA).

Results

Changes in soil C and N stocks

The rates of absolute stock changes varied greatly, exhibiting a normal distribution for C in both the organic and mineral layers and for N in the mineral layer. However, the distribution of N in the organic layer was not normal, probably as a result of the limited number of observations (Fig. 1). The mean rates of absolute stock change for the organic and mineral layers, respectively, were 34 (95% CI = 11.0) and 15 (95% CI = 22.4) g m^{-2} yr^{-1} for C, and 1 (95% CI = 0.3) and −2 (95% CI = 3.0) g m^{-2} yr^{-1} for N. This indicated that stocks of both C and N were significantly increased in the organic layer but not in the mineral layer. The mean rates of absolute stock change for total soil C and N were 50 (95% CI = 24.8) and −1 (95% CI = 3.0) g m^{-2} yr^{-1}, respectively, which indicated that, when all the studies were included, the total soil C stock increased following afforestation but the total N stock did not change.

Soil C and N stock changes had similar temporal patterns in either the organic or the mineral layer, but the temporal patterns

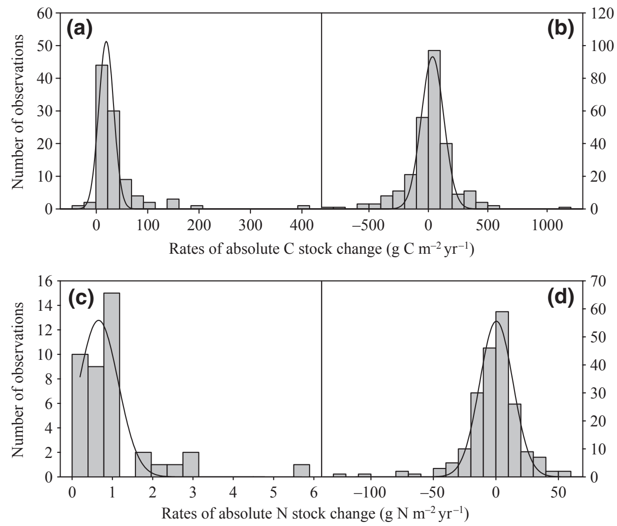

Fig. 1 Frequency distribution of: (a) rates of absolute C stock change (g m^{-2} yr^{-1}) in the organic layer (mean = 34.3, median = 22.7, 95% CI = 11.0, n = 97, r^2 = 0.96, P < 0.0001); (b) rates of absolute C stock change (g m^{-2} yr^{-1}) in the mineral horizon (mean = 15.2, median = 30.0, 95% CI = 22.4, n = 267, r^2 = 0.96, P < 0.0001); (c) rates of absolute N stock change (g m^{-2} yr^{-1}) in the organic horizon (mean = 1.0, median = 0.8, 95% CI = 0.3, n = 41, r^2 = 0.78, P < 0.0001); and (d) rates of absolute N stock change (g m^{-2} yr^{-1}) in the mineral horizon (mean = −2.1, median = 0.4, 95% CI = 3.0, n = 203, r^2 = 0.97, P < 0.0001). The curves were fitted by a Gaussian function.

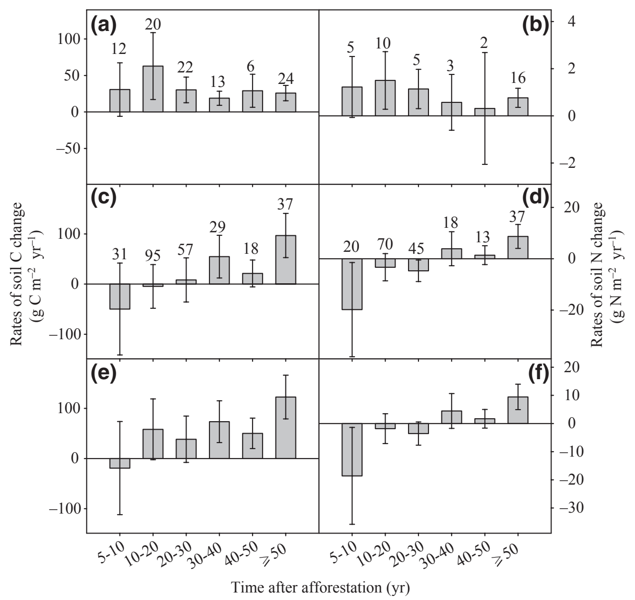

Fig. 2 Variation of rates of absolute stock change with ages of afforestation for: (a) soil C in the organic horizon; (b) soil N in the organic horizon; (c) soil C in the mineral horizon; (d) soil N in the mineral horizon; (e) total soil C; and (f) total soil N. The error bars represent 95% confidence intervals (CI) and values above the bars are the corresponding number of observations. The rates of absolute stock change for total soil C and N were not extracted directly from the literature but were the sums of mean rates of absolute stock change for mineral and organic layers for each category.

were different between the two layers (Fig. 2, Table S2). For the organic layer, the rates of absolute C and N stock changes tended to increase from the initial stage, reaching their highest values at 10–20 yr and then decreasing, but there was no significant difference between different stages. The mean rates of absolute stock change for C were all significantly greater than zero except for the 5–10 yr stage, but rates for N were more variable, likely because of the low number of observations (Fig. 2a,b). For the mineral layer, rates of soil C and N stock changes decreased initially during the early stage after afforestation; this was followed by a gradual return of stocks to the pre-afforestation values and then an increase to net gains of C and N (Fig. 2c,d). After the initial decrease, rates of absolute C and N stock changes increased linearly (P < 0.05) with the age of afforestation. At 5–10 yr after afforestation, stocks of both soil C and N were depleted but the changes were not significant for C. The temporal patterns for rates of total C and N stock changes were similar to those in the mineral layer (Fig. 2e,f). There seemed to be a time lag between soil C and N stock changes. As depicted in Fig. 2(e,f), total C stock changes were significantly greater than zero at 30–40 yr, but for total N there was no significant change until 50 yr after afforestation.

The effects of prior land use types, climate zone and planted tree species on soil C and N stocks changes after afforestation are given in Figs 3–5 and Table S3–S5. Soil C stocks increased in the organic and mineral layers, which in turn resulted in a significant increase in total C stock after cropland afforestation. The soil C stock increased significantly in the organic layer, but decreased significantly in the mineral layer, which, when

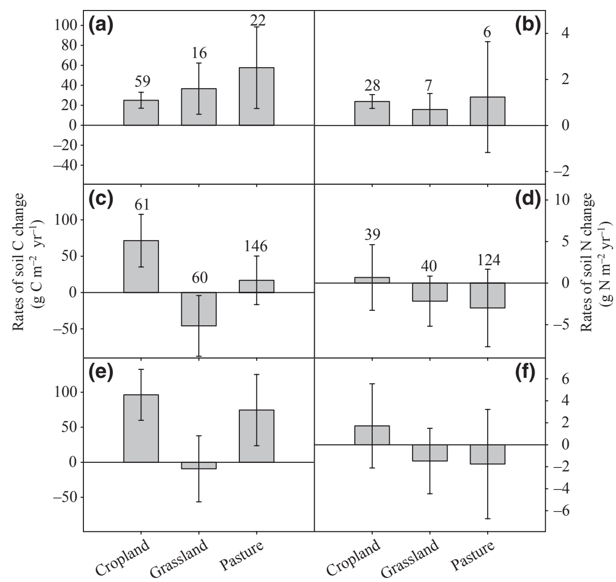

Fig. 3 Rates of absolute stock change following afforestation on cropland, grassland and pasture for; (a) soil C in the organic horizon; (b) soil N in the organic horizon; (c) soil C in the mineral horizon; (d) soil N in the mineral horizon; (e) total soil C; and (f) total soil N. The error bars represent 95% confidence intervals (CI) and values above the bars are the corresponding number of observations. The rates of absolute stock change for total soil C and N were not extracted directly from the literature but were the sums of mean rates of absolute stock change for mineral and organic layers for each category.

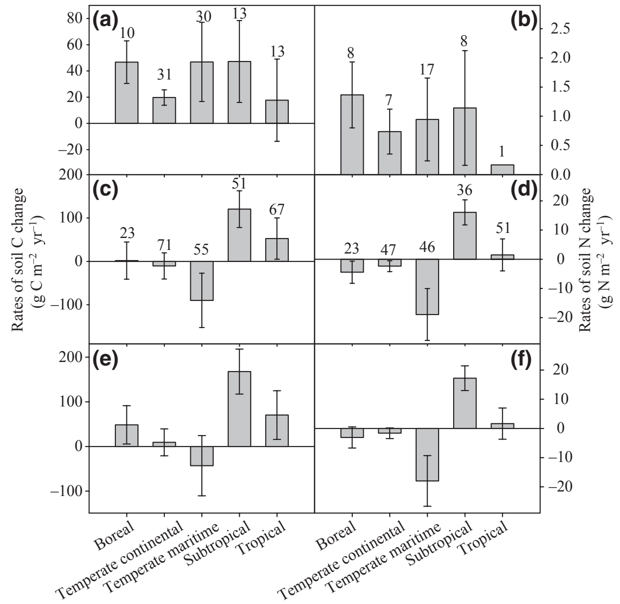

Fig. 4 Rates of absolute stock change following afforestation in different climatic zones for: (a) soil C in the organic horizon; (b) soil N in the organic horizon; (c) soil C in mineral horizon; (d) soil N in mineral horizon; (e) total soil C; and (f) total soil N. The error bars represent 95% confidence intervals (CI) and values above the bars are the corresponding number of observations. The rates of absolute stock change for total soil C and N were not extracted directly from literature but were the sums of mean rates of absolute stock change for mineral and organic layers for each category.

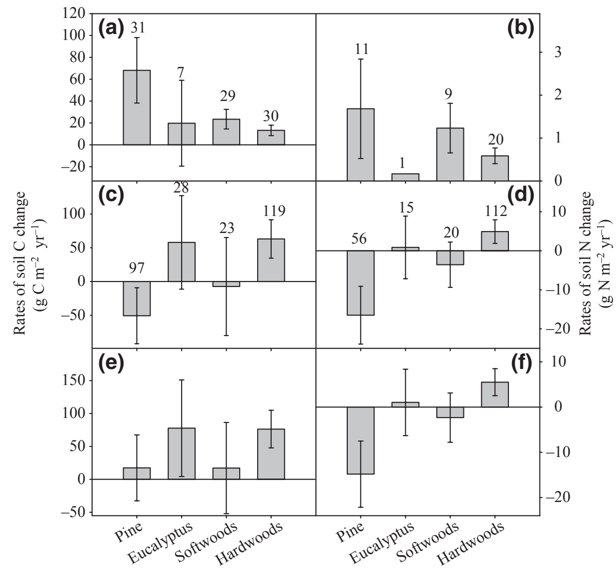

Fig. 5 Rates of absolute stock change following afforestation with different tree species: (a) soil C in the organic horizon; (b) soil N in the organic horizon; (c) soil C in the mineral horizon; (d) soil N in the mineral horizon; (e) total soil C; and (f) total soil N. The error bars represent 95% confidence intervals (CI) and values above the bars are the corresponding number of observations. The softwood and hardwood species categories exclude pine and Eucalyptus, respectively. The rates of absolute stock change for total soil C and N were not extracted directly from literature but were the sums of mean rates of absolute stock change for mineral and organic layers for each category.

combined, resulted in no change in total soil C stock after grassland afforestation (Fig. 3, Table S3). Pasture afforestation also significantly increased total C stock mainly as a result of the increase in C stock in the organic layer. Afforestation did not change total N stocks or N stocks in the mineral layer for all the three prior land use types, but afforestation increased the N stock in the organic layer for cropland (Fig. 3 and Table S3). Both C and N stocks in the organic layer increased, except in the tropical zone where the C stock was not changed (Fig. 4 and Table S4). In the mineral layer, soil C stocks after afforestation were unchanged in the boreal and temperate continental zones, decreased in the temperate maritime zone, and increased in the subtropical and tropical zones; soil N stocks were decreased in the boreal, temperate continental and temperate maritime zones, increased in the subtropical zone and unchanged in tropical zone. Total soil C stocks were increased in the boreal, subtropical and tropical zones but unchanged in the temperate continental and temperate maritime zones. For the total N stock, significant changes were found in the temperate maritime (decrease) and subtropical (increase) zones (Fig. 4, Table S4). With regard to tree species planted (Fig. 5, Table S5), soil C stocks in the organic layer were increased for pine, softwoods and hardwoods, with the stock in the pine plantation significantly higher than in the others, but they did not change for Eucalyptus. Soil N stocks in the organic layer tended to increase for all tree species (note that only one observation was available for Eucalyptus). For the mineral layer, both soil C and N stocks decreased for pine, and increased for hardwoods, but they did not change for the other two species. Total soil C increased for hardwoods including Eucalyptus, but did not change for softwoods including pine. Total soil N stock decreased for pine but increased for hardwoods, and did not change for Eucalyptus and softwoods.

Relationship between soil C and N stock changes

There was a significant relationship between the rates of absolute C and N stock changes in the organic layer (r^2 = 0.83, P < 0.0001, n = 41) and the mineral layer (r^2 = 0.66, P < 0.0001, n = 203) (Fig. 6a,b), indicating that soil C stock change was strongly related to N stock change, or vice versa. According to the relationship between rates of absolute C and N stock changes, each g of N gain was accompanied by 35 and 7 g gain of C for in organic and mineral layers, respectively. There was a stronger linear relationship between rates of relative C and N change in the mineral layer (r^2 = 0.80, P < 0.0001, n = 203) (Fig. 6c). Statistical analysis indicated that the slope (0.87) was significantly different from 1 (P < 0.01), implying that the rate of relative N stock change was smaller than that of relative C stock change in the mineral layer.

Discussion

Temporal patterns of soil C and N stock change

Although the mechanisms that control the post-agricultural rate of accumulation are different for C and N (McLauchlan, 2006),

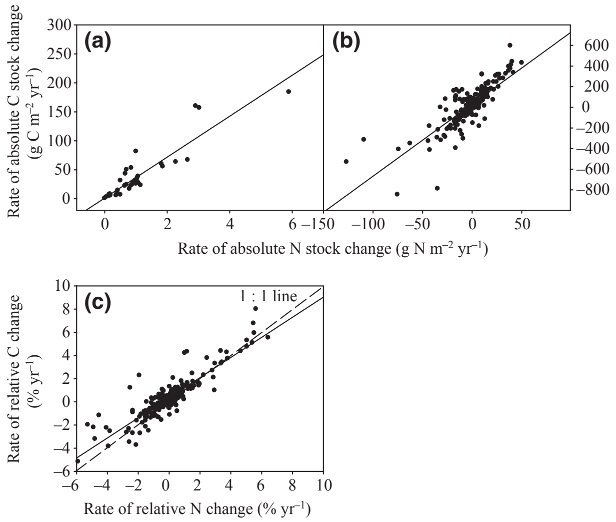

Fig. 6 Correlations between: (a) rates of absolute C stock change and rates of absolute N stock change in the organic horizon ($y = 35.3x + 1.3$, $r^2 = 0.83$, $P < 0.0001$, $n = 41$); (b) rates of absolute C stock change and rates of absolute N stock change in the mineral horizon ($y = 7.0x + 31.1$, $r^2 = 0.66$, $P < 0.0001$, $n = 203$); and (c) rates of relative C stock change and rates of relative N stock change in the mineral horizon ($y = 0.87x + 0.35$, $r^2 = 0.80$, $P < 0.0001$, $n = 203$). The dashed line in panel (c) denotes the 1 : 1 line.

similar temporal patterns of soil C and N stock changes following afforestation have been reported by a number of field studies, that is: (1) increase (Knops & Tilman, 2000; Morris *et al.*, 2007; Kirschbaum *et al.*, 2008; Mao *et al.*, 2010); (2) decrease (Hooker & Compton, 2003; Kirschbaum *et al.*, 2008; Smal & Olszewska, 2008); (3) negligible change (Bashkin & Binkley, 1998; Grigal & Berguson, 1998; Sartori *et al.*, 2007); (4) or an initial decrease in soil C or N during the early stage, followed by a gradual return of C or N stocks to pre-afforestation values and then an increase to net C or N gains (Markewitz *et al.*, 2002; Wang *et al.*, 2006; Huang *et al.*, 2007; Ritter, 2007; Mao *et al.*, 2010). The duration of the initial decrease in C was reported to last for 3–35 yr after agricultural abandonment (Paul *et al.*, 2002). In a review study, Paul *et al.* (2002) tried to determine the temporal pattern of C stock change with age. However, the derived pattern was not very clear, as different depths were mixed together and there was great difference among depths in terms of temporal C stock change. In spite of this, there was a significant net accumulation of soil C 30 years after afforestation (Paul *et al.*, 2002). Our study revealed that the temporal patterns were different for the organic and mineral layers; and the temporal patterns for both C and N stock changes in the mineral layer or for total C and N were similar to the pattern (4) described earlier in this section. Similar to the finding by Paul *et al.* (2002), our meta-analysis also indicated that there was a significant accumulation of C 30 yr after afforestation. In addition, our study showed that there was no significant increase of total soil N stock until 50 yr after afforestation.

As soil C content is determined by both the input and decomposition of plant litter, one possible reason for the initial decrease in soil C was that the input of C from the young stands was too low to match the ongoing decomposition of C inherited from agriculture (Vesterdal *et al.*, 2002). For this reason, there often is a time lag between plant production and soil C accumulation; for example, nearly all the increase in ecosystem C went into standing biomass, but not soil C, during 30 yr of forest development in North Carolina (Compton & Boone, 2000). Our study further revealed that the initial decrease was mainly caused by a decrease of C stock in the mineral layer.

Soil N stock change is a balance of N input (e.g. atmospheric N deposition, biological N fixation) and output (e.g. N uptake by plant, N emission to groundwater or the atmosphere). During forest development, N uptake per tree varies with age. N demand is generally higher in the phase of active growth before canopy closure for both hardwood and softwood forests (Kimmins, 2004). However, owing to the higher biomass in mature forest stands, total N accumulation is higher in old than in young forest stands (Johnson, 1992). If there are no sustainable N inputs, increasing N uptake during forest development and accumulation of N in standing biomass could result in a decrease in soil N pools. The underlying mechanisms of soil N stock change following afforestation are not well understood. To our knowledge, none of the relevant studies have clearly quantified the sources that explain N stock increase following afforestation or other land use change. The linear increase in the rates of absolute N stock change (after the initial decrease) indicated that there were long-term sources of N. For the agricultural systems, N fertilization is an important source of N input; however, N fertilization was applied only at very limited sites at the time of planting. Therefore, N fertilization cannot be used to explain the long-term increase in soil N. Atmospheric N deposition and biological N fixation are often used to explain the N increase following afforestation or during forest development (Knops & Tilman, 2000; Morris *et al.*, 2007; Yang *et al.*, 2011). Houlton *et al.* (2008) reported that biological N fixation rates (including both asymbiotic and symbiotic N fixation) were 2.2, 4.9 and 2.9 g N m^{-2} yr^{-1}, respectively, for boreal, temperate and tropical forests. Atmospheric N deposition rates varied from < 0.2 g N m^{-2} yr^{-1} in remote regions to > 5 g N m^{-2} yr^{-1} in some industrial regions or regions with intensive agriculture (Dentener *et al.*, 2006). However, some studies indicated that these sources could not explain the whole increase in soil N. For example, Morris *et al.* (2007) found that N deposition (including wet and dry deposition) and asymbiotic N fixation (which was assumed to 0.5 g N m^{-2} yr^{-1} at its maximum) could only explain 40–70% of the annual soil N increase in southwest Michigan's afforested sites. In sites with N-fixing plants, symbiotic N fixation may be an important source of soil N input (Knops & Tilman, 2000; Resh *et al.*, 2002). N redistribution within the soil profile, that is, mining of deeper soil N, has also been proposed as an alternative mechanism responsible for soil N increase after afforestation or forest development (Knops & Tilman, 2000); however, this source has not been quantified. Bedrock has been found to be an important source of N for terrestrial ecosystems (Holloway & Dahlgren, 1999; Holloway *et al.*, 2001; Morford *et al.*, 2011), and was reported to release 0.4–3.7 g N m^{-2} yr^{-1}

(Holloway *et al.*, 2001). The combination of these N sources (3–14 g N m^{-2} yr^{-1}) can roughly explain the observed N accrual in our study (9.5 ± 4.5 g N m^{-2} yr^{-1} when afforestation ≥ 50 years). However, future quantitative studies are still necessary to determine the contributions from potential N sources, which in turn will make it possible to unravel the underlying mechanisms of N stock increase after afforestation.

Effects of biophysical factors on soil C and N stock dynamics

Many factors have been found to influence C stock dynamics following afforestation, including site preparation, prior land use, climate, soil clay content, tree species planted, fertilizer application, and N_2 fixation (Paul *et al.*, 2002; Laganière *et al.*, 2010). But information on the factors affecting soil N stock dynamics is very scarce and uncertain. The current study indicates that the factors influencing C dynamics may also influence N dynamics.

Prior land use Land use has a great impact on both soil C and N dynamics. The dominant paradigms hold that cultivation of cropland result in sustained and larger losses of soil C and N relative to untilled grassland and forest (Davidson & Ackerman, 1993; McLauchlan, 2006). Upon the cessation of cultivation and afforestation, the new equilibrium will move to the forest. Unlike cropland, natural grassland continuously maintains vegetation cover on the soil, reduces soil temperatures, and can have high rates of productivity and turnover that add organic matter, particularly from below ground, to the soil (Brown & Lugo, 1990). Therefore, in the long term, grassland systems have nearly equivalent (Franzluebbers *et al.*, 2000) or higher (Tate *et al.*, 2000) potential to store soil C as forest. Compared with natural grassland, pasture involves removal of biomass from the system; therefore C accumulation is likely lower than that of natural grassland. This is supported by the significant increase in seen soil C after cropland afforestation but no clear change of total soil C stocks after natural grassland afforestation and no change of soil C stock in the mineral layer after pasture afforestation. However, soil N stock change after afforestation was much smaller than soil C stock change (Fig. 3). Consistent with our results, some previous reviews also reported that C stocks increased for cropland afforestation (Guo & Gifford, 2002; Paul *et al.*, 2002; Laganière *et al.*, 2010). Similarly, Poeplau *et al.* (2011) predicted that soil C stock increased by 83% in the mineral soil after 100 yr of cropland afforestation, whereas soil C showed losses even after 140 yr of grassland afforestation. By contrast, C stocks were found to decrease significantly after pasture afforestation (Guo & Gifford, 2002; Paul *et al.*, 2002), or to increase for both pasture and grassland (Laganière *et al.*, 2010). However, the category of 'pasture' included natural grassland in the review by Guo & Gifford (2002), whereas the organic layer was included and soil layers were combined for analysis – although only part of the selected sites reported data from the organic layer (Laganière *et al.*, 2010). These all increased the uncertainty of comparison.

Tree species planted Different effects of tree species on soil C and N stock change after afforestation have been reported. In spite of some discrepancy, most reviews agreed that C stock tended to decrease following afforestation with pine but increase following afforestation with hardwoods (Guo & Gifford, 2002; Paul *et al.*, 2002; Berthrong *et al.*, 2009). By including both the organic and mineral layers, our study indicated that total soil C stock did not change following afforestation with softwoods including pine, whereas it increased following afforestation with hardwoods including Eucalyptus. The only review to consider soil N dynamics in the mineral layer reported that soil N stock significantly decreased after pine plantation (Berthrong *et al.*, 2009), which is consistent with our results. C or N stock difference in the organic layer is largely regulated by species difference between above-ground litterfall inputs and outputs (or decomposition), which is mainly controlled by litter quality (Hobbie *et al.*, 2007). Compared with the leaves of Eucalyptus and hardwoods, the substrate quality of conifer needles is poorer, which leads to slower decomposition (Paul *et al.*, 2002). Accordingly, more C and N accumulate in the organic layer for conifer species, especially pine, which is clearly demonstrated in our study. Compared with the organic layer, C or N stock change in the mineral layer is not clear. The similar patterns suggest that there likely are some common mechanisms responsible for the difference among species in terms of their effects on soil C and N stock changes. In contrast to the organic layer, root biomass and turnover may be more important determinants for the accumulation of soil organic matter in forests than above-ground litter input (Guo & Gifford, 2002). There is a difference in above- and below-ground litter production between pine and hardwood species. For example, the amount of above-ground litter was > 35 times the dead root fraction in a tropical pine plantation, whereas for a paired broadleaf secondary forest, the standing stock of dead roots was higher than the above-ground litter stock (Cuevas *et al.*, 1991). Additionally, conifer root litter had lower N concentration, higher C : N ratio and lignin : N ratio, with much lower decomposition rate, compared with hardwoods (Silver & Miya, 2001), which could have lowered C and N accumulation in mineral soil at the pine sites. Other mechanisms have been proposed to explain the effect of species difference on soil C or N stock change, but they require more supporting evidence (Knops *et al.*, 2002; Hobbie *et al.*, 2007). For example, plant species have the potential to impact soil C pools and their dynamics through their influence on the physical protection of soil organic matter by the occlusion of soil aggregates or on the chemical protection of soil organic matter at the mineral surface (Hobbie *et al.*, 2007); plant species were also reported to have a potential impact on N input and losses through their interactions with herbivores and soil microbial decomposers as well as their symbiotic interactions with N-fixing bacteria (Knops *et al.*, 2002).

Climate Climate may affect soil C and N accumulation through biotic processes associated with the productivity of vegetation and decomposition of organic matter (Post *et al.*, 1985). At the global scale, both total litterfall input and decomposition rate decrease with increasing latitude (Vernon *et al.*, 1982; Zhang *et al.*, 2008). The large litter production in tropical forests is compensated for by rapid decomposition, which may lead to relatively low C and N accumulation rates as shown in the current study. In the cooler climate zones, the lower litterfall input and decomposition rate may result in lower soil C and N accumulation rates and longer soil C and N stock recovery. The present study shows that the net balance between soil C (or N) input and output, that is, the accumulation of soil C or N, is highest in the subtropical zone. Another plausible explanation for the lower soil C and N accumulation in the temperate maritime zone is the effect of the tree species planted. According to our dataset, pine was planted in 80% of the studies conducted in this zone, and 87% of the studies were in New Zealand and the UK, especially the former. Consistent with our analysis, Post & Kwon (2000) reported that there was a tendency for rates of C accumulation to increase from temperate regions to subtropical regions. According to Paul *et al.* (2002), soil C (to a depth of < 30 cm) increased in the tropical (1.59% yr^{-1}) and subtropical (0.54% yr^{-1}) zones and, to a lesser extent, in the continental moist zone (0.60% yr^{-1}), but there was a slight decrease in the soil C in temperate/Mediterranean-type climate (−0.02% yr^{-1}). However, a statistical analysis was not performed to determine if the rate of C stock change was significantly different from zero (Paul *et al.*, 2002). Unlike our analysis, a recent review reported that the relative change of soil C following afforestation decreased by 1.5% in the boreal zone, but increased by 7–17% in other climate zones, with the highest increase in the temperate maritime zone (Laganière *et al.*, 2010). However, as we have stated, soil layers were combined for analysis, although only part of the selected sites reported data from the organic layer, which may increase the uncertainty of comparison.

Implications of the strong interactions between C and N dynamics

Afforestation has been proposed as an effective method of C sequestration in order to slow down the increase in atmospheric CO_2. However, whether C sequestration by afforestation can be sustained is determined by the availability of N, since 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 terrestrial C sequestration is not accompanied by a simultaneous N gain, the system will become increasingly N-limited or will undergo progressive N limitation (Luo *et al.*, 2004). The present study indicates that C stock dynamics are closely coupled with N stock dynamics, as clearly demonstrated by the strong correlation between C and N stock changes (Fig. 6). Following afforestation, soil N stock tended to increase linearly with age, aside from an initial decrease. The increase in N stock will reduce N limitation and support long-term C sequestration. However, since the rate of relative N stock change was found to be lower than that of relative C stock change, the C : N ratio gradually increased (Fig. S3). This may result in the occurrence of progressive N limitation in the long term, reducing the rate of C sequestration.

Acknowledgements

This work was financially supported by the US National Science Foundation (NSF) (grants DEB 0743778, DEB 0840964, DBI 0850290, and EPS 0919466), and by the United States Department of Energy, Biological Systems Research on the Role of Microbial Communities in Carbon Cycling Program. The authors thank Ms Amy Oliver for assisting with editing of the English grammar.

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Supporting Information

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

Fig. S1 Comparison of equivalent mass corrected and uncorrected stock changes.

Fig. S2 Comparison of measured and calculated stocks to 100 cm.

Fig. S3 Relative change in C : N ratios in the mineral layer.

Table S1 Characteristics of individual studies included in this study

Table S2 Rates of absolute stock change with ages of afforestation for the organic layer, the mineral layer and the total soil profile

Table S3 Rates of absolute stock change following afforestation on cropland, grassland and pasture

Table S4 Rates of absolute stock change following afforestation in different climatic zones

Table S5 Rates of absolute stock change following afforestation with different tree species

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

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