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# Carbon accumulation in agricultural soils after afforestation: a meta-analysis

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## Abstract

Deforestation usually results in significant losses of soil organic carbon (SOC). The rate and factors determining the recovery of this C pool with afforestation are still poorly understood. This paper provides a review of the influence of afforestation on SOC stocks based on a meta-analysis of 33 recent publications (totaling 120 sites and 189 observations), with the aim of determining the factors responsible for the restoration of SOC following afforestation. Based on a mixed linear model, the meta-analysis indicates that the main factors that contribute to restoring SOC stocks after afforestation are: previous land use, tree species planted, soil clay content, preplanting disturbance and, to a lesser extent, climatic zone. Specifically, this meta-analysis (1) indicates that the positive impact of afforestation on SOC stocks is more pronounced in cropland soils than in pastures or natural grasslands; (2) suggests that broadleaf tree species have a greater capacity to accumulate SOC than coniferous species; (3) underscores that afforestation using pine species does not result in a net loss of the whole soil-profile carbon stocks compared with initial values (agricultural soil) when the surface organic layer is included in the accounting; (4) demonstrates that clay-rich soils (>33%) have a greater capacity to accumulate SOC than soils with a lower clay content (<33%); (5) indicates that minimizing preplanting disturbances may increase the rate at which SOC stocks are replenished; and (6) suggests that afforestation carried out in the boreal climate zone results in small SOC losses compared with other climate zones, probably because trees grow more slowly under these conditions, although this does not rule out gains over time after the conversion. This study also highlights the importance of the methodological approach used when developing the sampling design, especially the inclusion of the organic layer in the accounting.

*Keywords:* carbon sequestration, land use change, methodological approach, mixed linear model, soil organic carbon, soil properties, tree plantation

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#### Introduction

The carbon (C) contained in forest ecosystems accounts for a major proportion of the global terrestrial C stocks. It is estimated that the forest biomass contains more than 80% of all global C contained in the aboveground

Correspondence: Jérôme Laganière, Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., PO Box 10380, Stn. Sainte-Foy, Québec, Quebec, Canada G1 V 4C7, tel. + 1 418 648 4933, fax + 1 418 648 5849, e-mail: jlaganie@nrcan.gc.ca biomass and that forest soils contain more than 70% of the C contained in soils (Batjes, 1996; Jobbagy & Jackson, 2000; Six *et al.*, 2002a). Historically, terrestrial C pools have declined significantly due to land use changes and in particular due to deforestation, i.e. the conversion of forest environments to agricultural land (Jandl *et al.*, 2007). Following their transition to agricultural uses, forest environments experience a dramatic decline in C in response to the removal of plant biomass and the decrease in organic matter inputs to the soil consistent with deforestation, but also as a result of increased decomposition and erosion caused by soil disturbance (Six *et al.*, 2000; Murty *et al.*, 2002; Lal, 2005; McLauchlan, 2006).

On the other hand, the conversion of treeless land not previously forested into a plantation (afforestation sensu, Evans, 1992) has been cited as an effective method for reducing the atmospheric CO<sub>2</sub> concentration because of the ability to sequester C in vegetation and soil (IPCC, 2001; Jandl et al., 2007). Afforestation usually results in the establishment of a higher plant biomass that is perennial and has a longer rotation compared with crop plants that are harvested annually. In the soil, the presence of trees modifies the quality and quantity of litter inputs and microclimatic conditions such as moisture and temperature (Bouwman & Leemans, 1995). In addition, the cessation of tillage operations (plowing) generally reduces disturbance and provides better protection of soil organic carbon (SOC) against decomposition (Six et al., 2000; Del Galdo et al., 2003). The transition from agricultural soil to forest soil is also accompanied by a change in the soil microbial and faunal communities. A greater biodiversity of organisms, particularly the presence of earthworms, is believed to promote the formation of stable aggregates (Jégou et al., 2000).

Soil has a great capacity to store C; it contains more C than the combined amount present in both living plant biomass and atmospheric  $CO_2$  (Jobbagy & Jackson, 2000). The residence time of stable fractions of SOC can be >1000 years (von Lutzow *et al.*, 2006), making it a much more stable sink than living plant biomass, given that the average rotation time can be as short as 10 years, for example, for *Eucalyptus globulus* plantations in southwestern Australia (Mendham *et al.*, 2003).

Despite the considerable SOC sequestration potential that afforestation offers, many studies have reported contradictory findings. Afforestation resulted in either a decrease (Parfitt et al., 1997; Perrott et al., 1999; Ross et al., 1999; Farley et al., 2004) or an increase in SOC stocks (Del Galdo et al., 2003; Lemma et al., 2006; Grünzweig et al., 2007), or had a negligible effect (Bashkin & Binkley, 1998; Chen et al., 2000; Davis, 2001; Davis et al., 2007; Smal & Olszewska, 2008). Nevertheless, a trend appears to emerge: afforestation frequently shows an initial loss in SOC during the first few years, followed by a gradual return of C stocks to levels comparable to those in the control agricultural soil, and then increasing to generate net C gains in some cases (Romanya et al., 2000; Paul et al., 2002; Vesterdal et al., 2002; Turner et al., 2005; Wang et al., 2006; Davis et al., 2007; Huang et al., 2007; Ritter, 2007), but often lower than the values in a comparable natural forest (DeGryze et al., 2004; Smal & Olszewska, 2008). Apart from that, there is still no consensus in the scientific community concerning the factors determining the restoration of SOC stocks following afforestation.

The balance between C inputs in the form of litter (aboveground and belowground) and losses through decomposition determines whether the ecosystem is a sink or a source of C. Evaluating the C dynamics of this type of system requires data on the size of the C pool, the magnitude of the C input and output fluxes, as well as information about the mechanisms involved in controlling flux dynamics. To promote the C sink status of tree plantations, it is therefore imperative to determine the mechanisms involved in controlling SOC dynamics and more specifically in the storage of C in the soil after afforestation.

To date, three literature reviews have been devoted completely (Paul et al., 2002) or partly to this question (Post & Kwon, 2000; Guo & Gifford, 2002). Despite the limited number of studies available at that time, Paul et al. (2002) identified previous land use as the main determining factor, followed by climate and species planted, while Post & Kwon (2000) identified plant productivity, soil physical and biological properties, the history of C inputs and physical soil disturbance. More specifically, Guo & Gifford (2002) concluded that afforestation of pastureland does not affect C stocks when deciduous species are planted, but that C stocks decline when pine is used. However, when afforestation takes place on cropland, restoration of SOC stocks does occur. Unfortunately, much of the data used in the reviews cited above are derived from studies that were not designed specifically to investigate the question of the mechanisms involved in the dynamics of SOC stocks following afforestation (Paul et al., 2002). Also, given the limited number of studies available, some SOC stock estimates were made using approximated soil bulk density values in cases where the authors provided only the SOC concentrations. Consequently, the conclusions drawn from these literature reviews are limited by inappropriate experimental designs, sampling methods and/or soil analysis techniques (Paul et al., 2002). Since the publication of these reviews, more than 20 additional studies have been published. The availability of new studies designed specifically to answer this question provides an opportunity to more accurately test the involvement of these factors in the restoration of SOC stocks following afforestation.

The objective of this paper is to investigate the factors that influence the recovery of SOC stocks following afforestation of an agricultural soil. To achieve this objective, a series of factors known to affect soil C dynamics were selected and these factors are analyzed statistically using 33 recent publications (<20 years) specifically designed to answer this question. After a review of the literature on the subject, the following variables were chosen: (1) previous land use (cropland, pasture, natural grassland), (2) climatic zone, (3) soil properties (clay content, pH), (4) management options (preplanting disturbance, plantation density and tree species planted) and (5) methodological approaches (study design, sampling depth, plantation age, inclusion of the organic layer and of particles >2 mm). Each factor selected is examined in a separate section.

### Materials and methods

#### Study selection

The literature available on changes in SOC following afforestation of an agricultural soil was compiled. In this study, the term 'afforestation' refers to the establishment of a plantation (from seedlings or seeds) on treeless land where there has been no forest for at least 50 years and excludes natural regeneration without human intervention. The term 'agricultural' includes crops grown for food or fibre, permanent pastures and mixed agriculture (crop-pasture). Natural grasslands, which are ecosystems relatively undisturbed by human activity, were also added to the list of land uses for comparison purposes. In order to be included in this meta-analysis, the studies had to report the C content (mass of C per unit area and depth) of the mineral soil (or the SOC concentrations + soil bulk density) before and after afforestation. The studies that reported only SOC concentrations without bulk density values were excluded since bulk density can vary greatly following a change in land use (Murty et al., 2002) and as a function of plantation age (Vesterdal et al., 2002; Ritter, 2007). Moreover, only the studies including first-rotation plantations after the change in land use were retained. The purpose of this paper was not simply to include a large number of studies in the analysis, but rather to focus on the quality of those studies, i.e. those least likely to be biased owing to a lack of replications, exclusion of certain important variables, etc. Consequently, the data from 33 recent studies (<20 years) totalling 120 sites and containing nearly 200 observations were extracted and are analyzed in this paper (see Table 1 for more details). Of this data set, ten outlier values (value > 2x the standard deviation of the mean) were identified and therefore eliminated from the analysis. The exclusion of these outliers allowed to normalize the distribution of the data.

#### Analysis procedures

Given the variety of sampling depths used in the various studies and in order to facilitate comparison among the results, the data collected were divided into four depth categories: surface (0 to 10-15 cm), intermediate (0 to 20-30 cm), deep (> 30 cm) and total stock

(from 0 to > 30 cm). In the case of Six *et al.* (2002a), the A horizon sampled was considered in the intermediate depth category (Table 1). SOC stocks were not reported on an equivalent mass basis in any but one study. Not adjusting for equivalent mass of soil could result in a small bias in the estimation of changes in SOC stocks only when the entire topsoil is not sampled (if there is a significant amount of SOC beneath the maximum depth of sampling) (VandenBygaart & Angers, 2006). When the SOC content of the organic layer (LFH or O horizon) was reported (in 16 of the 33 studies; Table 1), a calculation with and without the layer could be made as a way of comparing sampling approaches. In addition to soil sampling depth and presence/absence of the organic layer in the calculation of SOC stock, other variables relating to the methodological approach were identified in each study: study design (paired sites, chronosequence or retrospective), plantation age (<10, 10-30 or >30 years) and soil size fractions considered (<2 or >2 mm). The following variables were also included to explain the accumulation of SOC stocks after afforestation: previous land use (cropland, pasture or natural grassland), climatic zone (boreal, temperate continental, temperate maritime, subtropical or tropical), clay content (low <33%, high  $\ge 33\%$ ), soil pH (low <5, moderate 5-7 or high >7), level of disturbance associated with preparation of the plantation site (low or high), plantation density (low < 1600 stems ha<sup>-1</sup>, high >1600 stems ha<sup>-1</sup>) and tree species planted (eucalyptus, pine, other coniferous trees or other broadleaf trees).

The effect of afforestation on SOC stocks was compared among the studies by using the change in the SOC stock after afforestation relative to the initial value of the SOC stock. This variable ( $\Delta$ STOCK%) was calculated as follows:  $\Delta$ STOCK% = ( $\Delta$ STOCK/iSTOCK) × 100; where  $\Delta$ STOCK (in Mg ha<sup>-1</sup>) represents the measured variation in the SOC stock after afforestation and iSTOCK (in Mg ha<sup>-1</sup>) refers to the initial value of the SOC stock before afforestation (retrospective design) or estimated from an adjacent control agricultural soil (paired sites or chronosequence). Since this variable can now be compared between different sites and different studies, a mixed linear model (PROC MIXED) was developed, including seven factors as fixed explanatory variables (previous land use, climatic zone, clay content, soil pH, pre-planting disturbance, plantation density and tree species planted; MODEL statement) and six factors representing potential different methodological approaches as random variables (study authors, study design, sampling depth, plantation age, inclusion of the organic layer and inclusion of particles >2 mm; RANDOM statement). By adding these random variables to the model, we can remove their effects on the dependent variable  $\Delta$ STOCK%. The

Previous			Plantation		Max. sampling			
land use	Location	Climate	Species	Age (years)	depth (cm)	Design	Obs	Reference
Cr	US	TR	Eucal	11.5	0–55	Р	4	Bashkin and Binkley (1998)
Cr	US	TR	Eucal	2.67	0–30	R	2	Binkley and Resh (1999)
Gr	NZ	TM	Pine	19	0-30 + O	Р	3	Chen et al. (2000)
Pa	NZ	TM	Pine	25	0–30	Р	2	Davis (2001)
Gr	NZ	TM	Pine	10	0–30	Р	2	Davis et al. (2007)
Cr	US	TM	Broad	10	0–50	Р	4	DeGryze et al. (2004)
Cr, Gr	IT	-	Broad	20	0–30	Р	4	Del Galdo et al. (2003)
Gr	EC	TM	Pine	5–25	0–10	С	3	Farley <i>et al.</i> (2004)
Pa	NZ	TM	Pine	13–30	0–10	Р	10	Giddens et al. (1997)
Pa	ME	-	Pine	35	0-50 + O	Р	6	Grünzweig et al. (2007)
Pa	AU	TM	Pine	16	0–100	Р	1	Guo et al. (2007)
Cr	US	TC	Broad	4–30	0 - 100 + O	С	4	Hansen (1993)
Gr	DE	TC	Broad	0–7	0–30	R	3	Jug et al. (1999)
Cr	ET	TR	Conif, broad	20	0-50 + O	Р	10	Lemma et al. (2006)
Cr	US	STR	Pine	3–14	0–50	С	12	Markewitz et al. (2002)
Pa	AU	TR	Broad	7–10	0 - 100 + O	Р	2	Mendham et al. (2003)
Cr	US	TC	Conif, broad	50, 53	0 - 100 + O	Р	10	Morris <i>et al</i> . (2007)
Pa	NZ	TM	Pine	20	0-20 + O	Р	4	Parfitt et al. (1997)
Cr	CA, US	TC	Conif, broad	21–49	0–100	Р	5	Paul et al. (2003)
Pa	CA	BO	Broad, pine	50	0-40 + O	Р	6	Pinno and Bélanger (2008)
Cr	US	TC	Pine	20, 46	0–10, 30–40 + O	R	5	Pregitzer and Palik (1997)
Gr	US	TC	Pine	32, 42	0-60 + O	Р	7	Quideau and Bockheim (1996)
Cr, Pa	US, PR	TR	Broad, eucal	7, 15	0–40	Р	20	Resh et al. (2002)
Cr	US	STR	Pine	35	0–60	R	2	Richter et al. (1999)
Pa	IS	BO	Broad	14–53	0–20	С	8	Ritter (2007)
Gr	NZ	TM	Pine	19	0-20 + O	Р	4	Ross et al. (1999)
Cr	US	STR	Pine	47	0-33 + O	С	2	Schiffman and Johnson (1989)
Cr	CA, US	TC	Pine, broad	29, 50	A horizon	Р	2	Six et al. (2002a)
Cr	DK	TC	Broad, conif	29, 200	0-25 + O	С, Р	9	Vesterdal et al. (2002)
Cr	CN	BO	Broad, pine	1–33	0 - 100 + O	С	10	Wang <i>et al</i> . (2006)
Gr	UK	TM	Conif	40	0-45 + O	Р	1	Zerva and Mencuccini (2005)
Gr	BR	TR	Eucal, pine	7, 20	0-60 + O	Р	21	Zinn <i>et al.</i> (2002)
Cr	US	TR	Eucal	10	0–25	С	1	Zou and Bashkin (1998)

 Table 1
 References included in the database for analysis of the factors that are responsible for restoring SOC stocks after afforestation

Previous land use abbrev: Cr, cropland; Pa, pasture; Gr, grassland.

Location abbrev: AU, Australia; BR, Brazil; CA, Canada; CN, China; DE, Germany; DK, Denmark; EC, Ecuador; ET, Ethiopia; IS, Iceland; IT, Italy; ME, Mediterranean; NZ, New Zealand; PR, Puerto Rico; UK, United Kingdom; US, United States.

Climate abbrev: BO, boreal; STR, subtropical; TC, temperate continental; TM, temperate maritime; TR, tropical; –, climate zone not considered because different from the five main zones.

Tree species abbrev: Conif, other coniferous; Broad, other broadleaf; Eucal, Eucalyptus.

Sampling depth abbrev: + O, information on the C stock of the organic layer was available.

Design abbrev: P, paired sites; C, chronosequence; R, retrospective.

Obs is the number of observations extracted per reference.

mixed model is written as follows:  $\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma} + \boldsymbol{\varepsilon}$ ; where  $\mathbf{y}$  represents a vector of observed data,  $\boldsymbol{\beta}$  is an unknown vector of fixed-effects parameters with known design matrix  $\mathbf{X}$ ,  $\boldsymbol{\gamma}$  is an unknown vector of random-effects parameters with known design matrix  $\mathbf{Z}$ , and  $\boldsymbol{\varepsilon}$  is an unknown random error vector. One issue in meta-analysis is that studies may differ widely in quality. All studies do not have the same quality and therefore should not be compared equally with each others. An interesting way to minimize the impact of this problem is to weight the analysis by some measure of quality. For that reason, the data were weighted (WEIGHT statement) as a function of sample size (n), as in most weighted meta-analyses. The WEIGHT

statement operates by replacing X'X and Z'Z with X'WX and Z'WZ, where W is the diagonal weight matrix. Since the data sets were not complete for all seven factors considered, the number of observations was specified on the figures for each level of the factor considered in the analysis. For this reason, although the interactions among the factors may be variables worth considering, they could not be examined in greater detail in this meta-analysis. The significant differences were detected using orthogonal contrast analysis (CONTRAST statement). The condition of normality of the data was verified using a combination of the Shapiro-Wilk, Cramer-von Mises and Anderson-Darling tests (PROC UNIVARIATE). Some other factors known to affect SOC dynamics (e.g. temperature, precipitation, nutrient availability, clay mineralogy, etc.) were not included in the analysis because of the colinearity with the other factors and because of the large quantity of missing data in the data set. All the statistical analyses were performed with SAS v. 9.1 (SAS Institute Inc., Cary, NC, USA) and the significance level was set at 0.05, unless otherwise indicated. The results of the mixed linear model are provided in Table 2.

#### **Results and discussion**

#### Previous land use

The land use history before afforestation can explain much of the variability in SOC contents (F = 6.54; P < 0.01). For each of the three categories of land use considered (cropland, pasture and natural grassland), afforestation had a much greater impact on previously cropped soils (Fig. 1). On average, afforestation resulted in an increase in SOC stocks of 26% for croplands, 3% for pastures, and <10% for natural grasslands; the two latter not being significantly different from zero. These results were also confirmed by a number of studies. Guo & Gifford (2002) estimated that afforestation of a soil previously used to grow crops results in SOC gains of 18%, but conversion of a pasture causes losses of 10%. Like us, they observed a difference in accumulation between cropland and pasture of around 25%. Similarly, Paul et al. (2002) observed an increase in SOC stocks in cropland, while a decrease was observed in the case of pastures.

The explanation for the difference in SOC accumulation between different land use categories appears to be a function of the similarities, or lack thereof, between the forest environment and the land use category in terms of their system components (i.e. the magnitude of the input and output fluxes, and the control mechanisms). The greater the difference in the agricultural system components compared with those of a forest **Table 2** Results of the mixed linear model developed toidentify the factors responsible for restoring SOC stocks afterafforestation of an agricultural soil (composed of seven fixedfactors and six random variables)

Covariable	Estimate		
Study authors			0
Sampling depth	6.28		
Inclusion of the organic layer	136.24		
Plantation age	68.53		
Inclusion of particles $>2 \text{ mm}$	0		
Study design	46.38		
Residuals			7218.95
Factor	df	F	Р
Previous land use	2	6.54	**
Climatic zone	4	1.81	+
Clay content	1	5.02	**
Soil pH (H <sub>2</sub> O)	2	1.07	ns
Preplanting disturbance	1	3.77	*
Plantation density	1	1.11	ns
Tree species planted	3	6.39	***

<sup>+</sup>*P*<0.10; \**P*<0.05; \*\**P*<0.01; \*\*\**P*<0.001;

ns, nonsignificant. The 'Estimate' column contains the variance component estimates for the six covariables, as well as the residual variance (method = REML).



**Fig. 1** Influence of previous land use on changes in SOC stocks after afforestation. The error bars are the standard errors of the mean. A different letter means a difference significant at P < 0.05. The number of observations is indicated in parentheses. The mean age of plantation is 23.3 years and the mean depth of sampling is 34.2 cm. SOC, soil organic carbon.

system, the greater the effect of afforestation will be on the restoration of SOC stocks. First, C inputs are generally lower in cropland than in forest ecosystems. The low NPP and annual harvesting of plant biomass in croplands reduces C inputs to the soil (Imhoff *et al.*, 2004). Second, the cropland system is generally char-

acterized by greater C losses due to soil disturbance (tillage). The various agricultural practices lead to different disturbance levels that affect SOC stocks in several ways. For example, mechanical disturbance caused by ploughing can increase the rate of decomposition of SOC by destroying the physical structure of the soil (Six et al., 1999; McLauchlan, 2006). Third, the mechanisms that contribute to SOC stabilization in the forest environment are often reduced under agricultural conditions. The abundance and diversity of macrofauna that promote the formation of stable aggregates can be very low in agricultural soils (Zou & Bashkin, 1998). The recalcitrance of C inputs (also known as 'biochemical protection' or 'selective preservation') is reduced in crop plants compared with forest trees (Lal, 2005; Cerli et al., 2006). Finally, other mechanisms that control flux dynamics differ between forest systems and cropland systems. For example, microclimatic conditions differ considerably between a forest environment and a cultivated field. The lack of forest cover increases soil temperature, thereby promoting C losses by microbial decomposition. For all the above-mentioned reasons, the state of equilibrium in the cropland system is generally maintained at lower SOC values than in forest environments, a reduction of approximately 20-40% on average compared with initial SOC values before deforestation (Mann, 1986; Ellert & Gregorich, 1996; Carter et al., 1998; Post & Kwon, 2000; Murty et al., 2002; Ogle et al., 2005). Consequently, afforestation has a very significant impact when carried out on a cropland soil. The increase in C inputs, the decrease in C losses and the reinforcement of the sequestration mechanisms associated with plantation establishment contribute to restoring SOC stocks. Plantation establishment shifts the equilibrium of the cropland system toward a forest system (toward higher SOC stocks). It can take approximately 40 years to achieve this equilibrium (Guo & Gifford, 2002), but in some cases it may be much longer (Cerli et al., 2006; Wang et al., 2006; Vesterdal et al., 2008).

Unlike the cropland system, afforestation has little impact on systems such as pastures and natural grasslands (Fig. 1). In a pasture, the soil is less disturbed and the disturbances tend to be related to grazing and trampling by livestock (cattle), although some pastures were ploughed and/or fertilized during their history. There are virtually no disturbances in natural grasslands as there is generally no human intervention. Indeed, a number of studies have shown that pasture and natural grassland soils could store as much, if not more, C than forest soils (Lugo & Brown, 1993; Corre *et al.*, 1999; Franzluebbers *et al.*, 2000; Garten & Ashwood, 2002). Unlike trees, in which most of the biomass is concentrated in the trunk, herbaceous plants allocate most of their biomass to the root system (Cerri *et al.*, 1991; Kuzyakov & Domanski, 2000; Bolinder et al., 2002). In addition, the turnover of this belowground (root) biomass is much faster than in forest environments (Kuzyakov & Domanski, 2000; Guo et al., 2007). Root C inputs are therefore higher in herbaceous than in forest ecosystems. Using soil cores and minirhizotrons, Guo et al. (2007) demonstrated that the roots of a grassland plant (Themeda triandra Forssk.) in Australia provide 3.6 Mg of  $C ha^{-1} yr^{-1}$  compared with 2.7 Mg of  $C ha^{-1} vr^{-1}$  for a *Pinus radiata* (D. Don.) forest. However, Yakimenko (1998) suggested that the dense root system of herbaceous plants limits water and gas exchanges, and thus limits the rate of decomposition. Overall, the impact of afforestation of previous pastures or grasslands on the accumulation of SOC is negligible and, in some cases, may even be negative. It is important to note that the average soil sampling depths are 34.1 cm for pastures and 26.1 cm for grasslands according to our meta-data. Therefore, our data set does not provide the information needed to address whether forests increase SOC at greater depths than the shallow measurement depths in the studies reviewed. Considering that the root system of trees is generally deeper than that of herbaceous plants, gains of SOC following afforestation in pastures or in natural grasslands cannot be excluded.

#### Climatic zone

The restoration of SOC stocks after afforestation was found to vary with climate zone (F = 1.81; P < 0.10).



**Fig. 2** Influence of different climatic zones on changes in SOC stocks after afforestation. The error bars are the standard errors of the mean. A different letter means a difference significant at P < 0.10. The number of observations is indicated in parentheses. The mean age of plantation is 22.9 years and the mean depth of sampling is 34.7 cm. BO, boreal; TC, temperate continental; TM, temperate maritime; STR, subtropical; TR, tropical. SOC, soil organic carbon.

Figure 2 shows that afforestation in the boreal zone results in average SOC losses of 1.5%, compared with gains ranging from 7% to 17% in the other climate zones; the temperate maritime zone shows the highest gains.

Based on Köppen's classification (McKnight & Hess, 2007), climate zones were classified for the purpose of this paper into five zones: boreal, temperate continental, temperate maritime, subtropical and tropical. The boreal zone includes the cool climates found mostly at northern latitudes between  $50^{\circ}$  and  $60^{\circ}$ , but up to  $70^{\circ}$ in the southern hemisphere. The mean annual temperature is generally below 4 °C. The temperate continental zone is located in the interior or on the east coast of the continents, extending from latitudes  $30^{\circ}$  to  $40^{\circ}$  or higher. This zone is characterized by hot summers and cold winters. The temperate maritime climate is characterized by hot, often rainy summers and mild winters. This climate zone is generally found on the west coast of the continents. The subtropical zone is located on both the coasts and interior of the continents between latitudes  $25^{\circ}$  and  $40^{\circ}$  ( $46^{\circ}$  in Europe), and is characterized by warm, humid summers. The tropical zone is characterized by proximity to the sea, low elevation and average annual temperatures >18 °C. Climate zones are therefore characterized not only by a given combination of mean annual temperature and total annual precipitation in a particular region, but also by other variables, such as proximity to the sea, regional topography, relative humidity and the seasonal characteristics of the region, which are factors likely to affect SOC dynamics.

The C contents of the Earth's main biomes vary from one biome to another, as well as from one compartment to another (plant vs. soil). Although heat and high precipitation contribute to a high NPP and a higher C accumulation in plant biomass than in other biomes, the climatic conditions in tropical regions stimulate decomposition and thus reduce SOC stocks (Lal, 2005). This makes the boreal biome the system with the greatest potential to store C, mainly in the form of SOC (Lal, 2005). Yet, the results of our analysis indicate that afforestation carried out in a boreal region has a small negative effect on SOC stocks. This trend may be explained by the slower tree growth and consequent low soil C input observed in the boreal biome. Indeed, this is the conclusion reached by Ritter (2007) during a study on afforestation with birch (Betula pubescens Enrh.) and larch (Larix sibirica Ledeb.) along a chronosequence of 97 years in Iceland. The author presumed that the processes responsible for changes in soil C content and in soil nutrients are slower in Iceland than in milder climate regions. Consequently, it would take >100 years to observe a significant increase in SOC contents in certain areas of the boreal zone. Thus, the

absence of a positive effect of afforestation in the boreal zone and the small SOC gains observed in the temperate continental zone are probably due to the relatively young age of the plantations which were on average 32 and 35 years, respectively. On the other hand, only 18.5 years on average is required to observe the greatest SOC accumulations in the temperate maritime climate. The high NPP may explain why such SOC gains are found shortly following afforestation under this climate.

## Soil properties

*Clay content.* Our analysis offers support for the theory that clay soils have a greater SOC accumulation potential after afforestation than coarse-textured soils (F = 5.02; P < 0.01). Figure 3 shows that soils containing a high proportion of clay (>33% clay) accumulate significantly more SOC after afforestation than soils lower in clay (<33% clay) where afforestation caused no change in SOC. Soils with high clay content accumulate approximately 25% more C upon afforestation than coarse-textured soils (Fig. 3).

Fine particles, particularly clays (particles  $< 2 \mu m$ ), are known to associate with organic compounds, thereby contributing to the formation of stable organomineral complexes. The physical protection (or 'spatial inaccessibility') against decomposition conferred by these stable complexes is believed to be an important mechanism that contributes to the stability of SOC (Blanco-Canqui & Lal, 2004; von Lutzow *et al.*, 2006). Despite this theoretical potential, few studies have clearly shown that texture plays a positive role in the



**Fig. 3** Influence of soil clay content on changes in SOC stocks after afforestation. The error bars are the standard errors of the mean. A different letter means a difference significant at P < 0.05. The number of observations is indicated in parentheses. The mean age of plantation is 24.6 years and the mean depth of sampling is 37.2 cm. SOC, soil organic carbon.



**Fig. 4** Influence of soil pH (H<sub>2</sub>O) on changes in SOC stocks after afforestation. The error bars are the standard errors of the mean. A different letter means a difference significant at P < 0.05. The number of observations is indicated in parentheses. The mean age of plantation is 20.1 years and the mean depth of sampling is 38.8 cm. SOC, soil organic carbon.

recovery of C stocks after afforestation (Paul *et al.*, 2002). Soil clay content may interact and be confounded with other factors that influence C storage such as drainage, primary productivity and initial SOC content.

pH. The statistical analysis results show an upward trend in SOC contents as soil pH increases (low pH = 10%, moderate pH = 13%, high pH = 22%; Fig. 4), but the variability of the data suggests a nonsignificant relationship (F = 1.07; P > 0.10). Soil pH can have various effects on soil C accumulation upon afforestation. Low pH can reduce tree growth and consequent C inputs to the soil. Low pH can also lead to SOC accumulation due to its effect in reducing decomposition rates of soil organic matter (Paustian et al., 1997). Soil pH is also believed to determine bioturbation activity of the soil and ultimately the formation of stable aggregates. After 120 years of natural regeneration on the Rothamsted experimental farm in England, Poulton et al. (2003) observed the formation of a litter layer at the Geescroft site (pH = 4.4), but not at the Broadbalk site (pH = 7.7). The authors attributed this to the fact that pedoturbators such as Lumbricus terrestris (L.) cannot survive in acidic soils (pH < 4.5).

# Management options

Although management in the forest environment is generally less intensive than in agriculture, there are several management strategies that can increase or reduce SOC stocks in plantations.



**Fig. 5** Influence of preplanting disturbances (left) and plantation density (right) on changes in SOC stocks after afforestation. The error bars are the standard errors of the mean. A different letter means a difference significant at P < 0.05. The number of observations is indicated in parentheses. On the left side of the figure, the mean age of plantation is 19.9 years and the mean depth of sampling is 30.5 cm. On the right side of the figure, the mean age of plantation is 21.4 years and the mean depth of sampling is 25.7 cm. LoDi, low intensity disturbances; HiDi, high intensity disturbances; LoDe, low density; HiDe, high density; SOC, soil organic carbon.

Preplanting disturbance. The analysis reveals a significant difference between the two preplanting disturbance regimes (F = 3.77; P < 0.05). We noted an increase in SOC stocks of 19% and 4% for sites that experienced low and high pre-planting disturbance, respectively (Fig. 5). Hence, minimizing the disturbances associated with the preparation of the plantation site can increase SOC stocks by 15%. Together with the low NPP of the newly established plantation, disturbances associated with tillage operations are believed to be responsible for SOC losses in the first few years following afforestation (Turner & Lambert, 2000). The disturbances associated with preparation of the plantation site were divided into two categories of intensity: low and high. Low intensity disturbances are those that do not involve intensive soil preparation or where hand planting was used, while high intensity disturbances describe sites that received mechanical soil preparation (plowing, mounding, trenching) and/or where machinery was used for tree planting. Since mechanical soil preparation increases the spatial variability of SOC, this makes it more difficult to detect a change in SOC stocks (Paul et al., 2002).

*Plantation density.* The results of our study show no impact of plantation density on changes in SOC after afforestation (F = 1.11; P > 0.10). We noted a nonsigni-



**Fig. 6** Influence of tree species planted on changes in SOC stocks after afforestation. The error bars are the standard errors of the mean. A different letter means a difference significant at P < 0.05. The number of observations is indicated in parentheses. The mean age of plantation is 23.3 years and the mean depth of sampling is 34.2 cm. Eucal, *Eucalyptus spp.;* Conif, coniferous (excluding pine); Broad, broadleaf excluding *Eucalyptus spp.*); SOC, soil organic carbon.

ficant increase in SOC stocks of 15% each for low and high densities, compared with an agricultural soil (Fig. 5). Tree planting density has an impact on soil microclimatic conditions (temperature, moisture) and the quantity of litter produced in the plantation. These factors ultimately affect the rate of decomposition, as well as soil C inputs. A high plantation density increases soil C inputs and accelerates forest canopy closure, which will have the effect of promoting the accumulation of organic matter in the soil. Hence, when SOC sequestration is one of the objectives of the plantation project, Turner et al. (2005) recommend increasing the initial plantation density in order to maximize short-term production. However, consistent with our findings, several recent studies did not observe any differences in terms of the impact of plantation density on SOC stocks (Binkley & Resh, 1999; Davis et al., 2007).

*Tree species planted.* A number of studies have shown that the tree species planted can have a major effect on the recovery of the SOC pool following afforestation (Resh *et al.*, 2002; Vesterdal *et al.*, 2002; Paul *et al.*, 2003; Lemma *et al.*, 2006). Our meta-analysis comes to similar conclusions (F = 6.39; P < 0.001; Fig. 6). An increase in SOC stocks of approximately 12% is observed when *Eucalyptus* spp. and *Pinus* spp. are used, while planting broadleaf trees (excluding *Eucalyptus* spp.) is associated with an increase of more than 25% (significantly different from zero), whereas planting coniferous trees (excluding *Pinus* spp.) has little effect on SOC stocks (2%).

The tree species planted have the potential to influence the magnitude and dynamics of SOC stocks because of the variability in their C inputs (quantity and quality) and potential losses. In fact, species characteristics regulate SOC storage by controlling C assimilation, transfer and storage in the belowground biomass, and its release through soil respiration, leaching and fire (De Deyn et al., 2008). The accumulation of an organic horizon (LFH or O horizon) is largely influenced by the difference between inputs via litterfall and losses through decomposition, and therefore differs significantly between species (Binkley & Giardina, 1998). For instance, according to the present meta-data, the contribution of the organic layer to changes in SOC after an average of 22 years following afforestation is 57% for *Pinus* spp., 52% for broadleaf species (excluding Eucalyptus spp.), 46% for coniferous species (excluding Pinus spp.), and only 16% for Eucalyptus spp. The influence of species on SOC dynamics in the mineral horizon is more complex. In fact, the tree species can affect three mechanisms of SOC stabilization in mineral soil: biochemical recalcitrance (or 'selective preservation'), chemical stabilization (or 'interactions with surfaces and metal ions') and physical protection (or 'spatial inaccessibility') (Sollins et al., 1996; Six et al., 2002b; von Lutzow et al., 2006). Through these mechanisms, the tree species therefore affect the accumulation and maintenance of SOC stocks in a stand.

Coniferous trees and broadleaf trees have different biomass allocation strategies. In fact, broadleaf trees generally have a larger and more deeply anchored root system (Strong & La Roi, 1983). A higher belowground biomass should therefore generate higher SOC inputs originating from the roots. In addition, since most of the study sites with coniferous trees (covered in this meta-analysis) tend to be associated with cooler climate zones, the probability of detecting a change in SOC stocks (see Smith, 2004) is lower because of the low plant growth in these regions. Hence, Turner & Lambert (2000) demonstrated a reduction in SOC stocks in coniferous plantations.

Pine species are thought to have a limited capacity to increase soil C stocks after planting, as lower SOC values than agricultural soils have been observed on pine afforested soils (Giddens *et al.*, 1997; Guo & Gifford, 2002; Markewitz *et al.*, 2002; Guo *et al.*, 2007). However, in many of these studies, the organic layer was not taken into consideration in estimates of SOC contents. Along with Kirschbaum *et al.* (2008), the present meta-analysis suggests that when considering the whole soil-profile carbon stocks, i.e. when the surface organic layer is included as part of the soil, pine afforestation would have the potential to sequester SOC (Fig. 6).

Species that have a higher root biomass-aboveground biomass ratio have a greater tendency to sequester SOC in

the deep soil horizons, which contributes to better protection of SOC against decomposition (Lorenz & Lal, 2005; Skjemstad et al., 2008). Seely et al. (2002) suggest that the selection of tree species for plantation offers the possibility of maximizing either SOC storage or woody biomass production. However, there is a compromise between these two extremes. The presence of nitrogenfixing species would also be one way of increasing SOC contents in plantations. According to the meta-analysis conducted by Johnson & Curtis (2001), the presence of nitrogen-fixing species in the stand is associated with an average increase in SOC stocks of >30% compared with stands that do not contain these species. Selecting several different species for the plantation (mixed stand) could also increase SOC stocks if the various species selected are functionally complementary (Fornara & Tilman, 2008). Unfortunately, few studies have explored this option in an afforestation context.

# Methodological approaches

Study design. Generally speaking, there are three types of study design: paired sites, chronosequence and retrospective design. Paired sites allow a comparison between a plantation and an adjacent control agricultural site. This approach has the advantage of allowing comparisons among several treatments (fertilization, density, thinning, species, etc.) and abiotic conditions (climate, topography, drainage, etc.). This type of study design is also very simple and inexpensive to develop. The disadvantages are the uncertainty concerning the uniformity of certain variables assumed to be fixed among the different sites (plantations and controls), as well as the fact that the sampling constitutes a single measurement in time. This problem can be partially solved by extending the paired sites design to a chronosequence. A chronosequence is the combination of a series of paired sites, once again with supposedly similar conditions, spread out over time to simulate plant succession. The basic assumption of his method is that each site in the sequence differs only in age and that each has the same biotic and abiotic history. The validity of this method has recently been called into question since many studies that use this method failed to validate the basic premise (Johnson & Miyanishi, 2008). At best, when the authors attempted to offer any justification for this assumption, the only information provided concerned the similarity of the type of substrate or topography (Johnson & Miyanishi, 2008). Finally, a retrospective design re-samples the same soils over a given period of time (repeated measurements). This is probably the most powerful and least biased design, since it eliminates the variation of error associated with different conditions between sites in the paired design and chronosequence, but it requires a greater investment in development. It also takes longer to obtain the results since changes in SOC stocks are observable only after several years.

Based on an estimate of the covariance parameters, study design appears to explain a large part of the variation in the changes in SOC after afforestation (Table 2). Of all the studies considered in this meta-analysis, most used the paired sites method (65%). According to the meta-data, the mean change in SOC stocks after afforestation for the different study designs is a gain of 8.8% for the paired sites, 2.0% for the chronosequence and a loss of 3.6% for the retrospective design. Consequently, the paired sites design seems to overestimate the change in SOC stocks by 12.4% relative to the retrospective design. The fact that the basic assumption of similar site conditions was not validated may be the source of this difference, but the exact reason is not well understood. This overestimation does not appear to originate from a difference in the plantation age between the study designs because these values are similar (an average of 23 and 24 years for the paired sites and the retrospective designs, respectively).

Soil sampling depth. Soil sampling depth is an important factor to consider when designing a sampling plan. There are a number of reasons that argue in favour of using a sampling plan that emphasizes collecting the deepest possible soil samples in order to accurately estimate total SOC stock. For instance, the studies that sampled only the surface horizon underestimated the SOC stocks of plantations, considering the fact that trees have a deeper root system than crop plants or grassland plants. Also, agricultural practices such as plowing can disturb the soil up to a depth of 40 cm, and plowing effects on soil C can be observed even below the plowing depth (Angers & Eriksen-Hamel, 2008). Moreover, it is also important to sample below the plow layer (Ap horizon) since we would not expect the SOC of the undisturbed deep horizon to react the same way following afforestation. The stability and mean residence time of SOC increase with soil depth (Lorenz & Lal, 2005). The soil sampling depths represented in our meta-data ranged from 7 to 100 cm, with an average of 34.2 cm. In spite of this large range, estimation of the covariance parameters shows that sampling depth does not explain a significant proportion of the data (Table 2).

*Plantation age.* Plantation age is an important factor to consider when estimating SOC stocks in a forest environment. In the first few years following plantation establishment, a reduction in SOC stocks was frequently observed (Paul *et al.*, 2002). As the plantation ages, the increase in the quantity of C inputs, accompanied by a

new microclimatic regime (Bouwman & Leemans, 1995) and enhanced organic matter protection (Six et al., 2002a; Del Galdo et al., 2003) promote SOC accumulation. Consequently, when the estimation of SOC contents is not repeated over time (e.g. paired sites design), plantation age can lead to biased results depending on whether the system sampled is in equilibrium or not. For example, sampling carried out in the first few years after afforestation would lead to an underestimation of SOC stocks in the plantation compared with agricultural soil because of the C losses directly associated with disturbance during preparation of the plantation but most likely related to the low NPP in the first few years following afforestation. Estimating the model's covariance parameters also reveals that plantation age is a major variable for explaining the variability in the data of the meta-analysis (Table 2). Indeed, the mean changes in SOC stocks increase with the different age classes, from losses of 5.6% in 'younger' plantations (<10 years), to gains of 6.1% and 18.6% in 'medium-aged' (10-30 years) and 'older' (>30 years) plantations, respectively, according to the meta-data. This is in agreement with the observation that initial loss in SOC occurs during the first few years after afforestation, followed by a gradual return of C stocks to levels comparable to those in the control agricultural soil, and then increasing to generate net C gains (Romanya et al., 2000; Paul et al., 2002; Vesterdal et al., 2002; Turner et al., 2005; Wang et al., 2006; Davis et al., 2007; Huang et al., 2007; Ritter, 2007).

Inclusion of the organic layer. According to most soil classification systems (e.g. Canadian, USDA, FAO), a soil is defined as 'the naturally occurring, unconsolidated mineral or organic material that occurs at the Earth's surface and is capable of supporting plant growth.' Consequently, the organic layer or LFH layer or O horizon is an integral part of the soil and failing to include it in the calculation of SOC stocks results in an underestimation of SOC stocks. Unlike herbaceous plants, most of the C returned to the soil by trees comes from litterfall (Richter et al., 1999; Scott et al., 1999). For instance, 115 years after the abandonment of agriculture in the northwestern United States, the C accumulated in the organic layer accounted for 71% of the total SOC stock of the forest (Hooker & Compton, 2003). According to the present meta-data, the contribution of the organic layer to the changes in SOC after an average of 22 years following afforestation is 47% and the contribution of this layer to total SOC stocks accounts for 17%. Nevertheless, it is important to point out that the SOC stored in the organic layer will always be more vulnerable to loss by disturbances such as fire than the SOC stored in the mineral layer. Although less stable than the C contained in the mineral layer, some of the C in the organic layer will, over the years, tend to migrate to the deep horizons of the mineral soil, where it will become more stable (Cole *et al.*, 1977; Kaiser & Guggenberger, 2003; Cerli *et al.*, 2006). However, owing to a multitude of factors, the turnover of the organic layer decreases with time and results in a significant long-lived C pool (Hooker & Compton, 2003).

The above-mentioned consideration raises the question as to whether the differences in results observed among the various studies concerning the ability of afforestation to restore SOC stocks may not be largely due to a methodological difference, i.e. whether or not the organic layer is taken into consideration in the analysis of SOC stocks. A number of studies show that this may indeed be the case. In fact, including the organic layer of the soil, and specifically the litter layer, frequently changes our picture of the soil of a plantation from a system that generates C losses to one that stores more C compared with the control agricultural soil (e.g. Chen et al., 2000; Wang et al., 2006). The studies that included the organic layer in their calculation generally reported a significant increase in SOC contents after afforestation. Of the covariance parameters estimated by the statistical analysis, the covariable 'inclusion of the organic layer' is the one that explains the greatest proportion of the variability in the data set (Table 2). Consequently, of all the factors that influence the restoration of SOC stocks, inclusion of the organic layer is a major methodological factor.

In practical terms, when the organic layer is to be included in the calculation of SOC stocks, the 0 cm level should be set at the organic–mineral layers interface. Hence, the entire organic layer should be sampled independently of the soil sampling depth planned in the sampling design.

Inclusion of particles >2 mm. SOC stocks were traditionally estimated by analyzing the C concentration of soil samples after sieving through a 2-mm mesh sieve. However, it has been suggested that using this approach could underestimate the C content of forest soils compared with agricultural soils, since trees generally have coarser roots than crop, pasture or grassland plants. In forest soils, a larger proportion of SOC is therefore found in the  $>2 \,\mathrm{mm}$  fraction. Consequently, some authors have opted for a methodology that includes particles larger than 2 mm (generally 5 mm) for their estimation of SOC stock (Mendham et al., 2003; DeGryze et al., 2004; Wang et al., 2006; Ritter, 2007). However, according to the estimation of the covariance parameters (Table 2), the inclusion of particles  $>2 \,\mathrm{mm}$ in the analysis method did not make any difference, at least according to the studies selected for this meta-analysis.

#### Conclusion

Based on this meta-analysis, it appears that the major factors that are responsible for restoring SOC stocks after afforestation are: previous land use, tree species planted, soil clay content, pre-planting disturbance and, to a lesser extent, climatic zone. However, the data extracted from the various studies did not enable us to determine whether a return to forest soil conditions (in terms of carbon stocks) is achieved after establishment of a plantation. Some studies, including those by DeGryze *et al.* (2004) and Smal & Olszewska (2008), suggest that SOC stocks rarely return to levels characteristic of the (undisturbed) natural forest. Even after several years, the SOC contents of a plantation are not equivalent to the levels found in a comparable natural forest.

Specifically, this meta-analysis indicates that the positive impact of afforestation on SOC stocks is more pronounced in cropland soils than in pastures or grasslands. The magnitude of this impact could be predicted by comparing the various systems in terms of their system components, i.e. the greater the difference in the agricultural system components compared with those of a forest system, the greater the effect of afforestation will be on the restoration of SOC stocks. It suggests that broadleaf tree species have a greater capacity to accumulate SOC, probably because of the higher root biomass-aboveground biomass ratio of broadleaf trees compared with coniferous trees. It underscores that afforestation using pine species does not results in net SOC losses compared with initial values (agricultural soil) when considering the whole soil-profile C in the calculation of SOC stocks; the losses of C in the mineral layer being compensated by gains in the organic layer. It shows that clay-rich soils (>33%) have a greater capacity to accumulate SOC than soils with a lower clay content (<33%). It indicates that minimizing pre-planting disturbances may increase the rate at which SOC stocks are replenished. Finally, it suggests that afforestation carried out in the boreal climate zone results in small SOC losses compared with other climate zones, probably because trees grow more slowly under these conditions, although this does not rule out the possibility that net SOC gains may be observed, but merely indicates that the period of time required to observe a change in SOC stocks could be longer than the average time after afforestation commonly used in the studies (32 years).

Understanding the factors that affect the global C cycle is essential to increasing our ability to predict and mitigate the consequences of climate change. We emphasize that particular attention should be paid to

the development of the sampling design in order to minimize the potential bias brought by different methodological approaches. It would appear that much of the variability in the results observed may be explained by such factors as whether or not the organic layer is included in the calculation of SOC stocks, plantation age, and study design.

We thus recommend that future research includes the organic layer in the calculation of SOC stocks or at least an estimate of its contribution to SOC stocks. We also recommend sampling the soil periodically after afforestation to determine whether the soil C status has reached equilibrium. This is especially important in colder climates (boreal and temperate continental) where the period of time required to compensate the losses of SOC associated with plantation establishment may be quite long (from 35 to >100 years). Finally, we suggest using the retrospective study design whenever possible because the paired sites and the chronosequence seem to overestimate the change in SOC stocks relative to the retrospective design. If the paired sites and the chronosequence are to be used, special attention should be paid to validating the basic assumption of similar site conditions.

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#### References

- Angers DA, Eriksen-Hamel NS (2008) Full-inversion tillage and organic carbon distribution in soil profiles: a meta-analysis. *Soil Science Society of America Journal*, **72**, 1370–1374.
- Bashkin MA, Binkley D (1998) Changes in soil carbon following afforestation in Hawaii. *Ecology*, **79**, 828–833.
- Batjes N (1996) Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science*, **47**, 151–163.
- Binkley D, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. *Biogeochemistry*, 42, 89–106.
- Binkley D, Resh SC (1999) Rapid changes in soils following Eucalyptus afforestation in Hawaii. Soil Science Society of America Journal, 63, 222–225.
- Blanco-Canqui H, Lal R (2004) Mechanisms of carbon sequestration in soil aggregates. Critical Reviews in Plant Sciences, 23, 481–504.
- Bolinder MA, Angers DA, Bélanger G, Michaud R, Laverdière MR (2002) Root biomass and shoot to root ratios of perennial

forage crops in eastern Canada. *Canadian Journal of Plant Science*, **82**, 731–737.

- Bouwman AF, Leemans R (1995) The role of forest soils in the global carbon cycle. In: *Carbon forum and functions in forest soils* (eds McFee W, Kelly JM), pp. 503–525. Soil Science Society of America, Madison, WI.
- Carter MR, Gregorich EG, Angers DA, Donald RG, Bolinder MA (1998) Organic C and N storage, and organic C fractions, in adjacent cultivated and forested soils of eastern Canada. *Soil and Tillage Research*, **47**, 253–261.
- Cerli C, Celi L, Johansson MB, Kogel-Knabner I, Rosenqvist L, Zanini E (2006) Soil organic matter changes in a spruce chronosequence on Swedish former agricultural soil I. Carbon and lignin dynamics. *Soil Science*, **171**, 837–849.
- Cerri CC, Volkoff B, Andreaux F, Leopoldo PR (1991) Nature and behaviour of organic matter in soils under natural forest, and after deforestation, burning and cultivation, near Manaus. *Forest Ecology and Management*, **38**, 247–257.
- Chen CR, Condron LM, Davis MR, Sherlock RR (2000) Effects of afforestation on phosphorus dynamics and biological properties in a New Zealand grassland soil. *Plant and Soil*, **220**, 151–163.
- Cole VC, Innis GS, Stewart JWB (1977) Simulation of phosphorus cycling in semiarid grasslands. *Ecology*, **58**, 1–15.
- Corre MD, Schnabel RR, Shaffer JA (1999) Evaluation of soil organic carbon under forests, cool-season grasses and warm-season grasses in the northeastern US *Soil Biology and Biochemistry*, **31**, 1531–1539.
- Davis M (2001) Soil properties under pine forest and pasture at two hill country sites in Canterbury. *New Zealand Journal of Forestry Science*, **31**, 3–17.
- Davis M, Nordmeyer A, Henley D, Watt M (2007) Ecosystem carbon accretion 10 years after afforestation of depleted subhumid grassland planted with three densities of *Pinus nigra*. *Global Change Biology*, **13**, 1414–1422.
- De Deyn GB, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.
- DeGryze S, Six J, Paustian K, Morris SJ, Paul EA, Merckx R (2004) Soil organic carbon pool changes following land-use conversions. *Global Change Biology*, **10**, 1120–1132.
- Del Galdo I, Six J, Peressotti A, Cotrufo MF (2003) Assessing the impact of land-use change on soil C sequestration in agricultural soils by means of organic matter fractionation and stable C isotopes. *Global Change Biology*, **9**, 1204–1213.
- Ellert BH, Gregorich EG (1996) Storage of carbon, nitrogen and phosphorus in cultivated and adjacent forest soils of Ontario. *Soil Science*, **161**, 587–603.
- Evans J (1992) *Plantation Forestry in the Tropics*, 2nd edn. Oxford University Press, New York, NY.
- Farley KA, Kelly EF, Hofstede RGM (2004) Soil organic carbon and water retention following conversion of grasslands to pine plantations in the Ecuadoran Andes. *Ecosystems*, 7, 729–739.
- Fornara DA, Tilman D (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology*, **96**, 314–322.
- Franzluebbers AJ, Stuedemann JA, Schomberg HH, Wilkinson SR (2000) Soil organic C and N pools under long-term pasture

management in the Southern Piedmont USA. *Soil Biology and Biochemistry*, **32**, 469–478.

- Garten CT Jr, Ashwood TL (2002) Landscape level differences in soil carbon and nitrogen: implications for soil carbon sequestration. *Global Biogeochemical Cycles*, **16**, 1114, doi: 10.1029/2002GB001918.
- Giddens KM, Parfitt RL, Percival HJ (1997) Comparison of some soil properties under *Pinus radiata* and improved pasture. *New Zealand Journal of Agricultural Research*, **40**, 409–416.
- Grünzweig JM, Gelfand I, Fried Y, Yakir D (2007) Biogeochemical factors contributing to enhanced carbon storage following afforestation of a semi-arid shrubland. *Biogeosciences*, 4, 891–904.
- Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. *Global Change Biology*, **8**, 345–360.
- Guo LB, Wang MB, Gifford RM (2007) The change of soil carbon stocks and fine root dynamics after land use change from a native pasture to a pine plantation. *Plant and Soil*, **299**, 251–262.
- Hansen EA (1993) Soil carbon sequestration beneath hybrid poplar plantations in the North Central United States. *Biomass and Bioenergy*, **5**, 431–436.
- Hooker TD, Compton JE (2003) Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. *Ecological Applications*, **13**, 299–313.
- Huang M, Ji JJ, Li KR, Liu YF, Yang FT, Tao B (2007) The ecosystem carbon accumulation after conversion of grasslands to pine plantations in subtropical red soil of south China. *Tellus Series B-Chemical and Physical Meteorology*, **59**, 439–448.
- Imhoff ML, Bounoua L, Ricketts T, Loucks C, Harriss R, Lawrence WT (2004) Global patterns in human consumption of net primary production. *Nature*, 429, 870–873.
- IPCC (2001) Third Assessment Report. Climate Change 2001. Cambridge University Press, Cambridge.
- Jandl R, Lindner M, Vesterdal L *et al.* (2007) How strongly can forest management influence soil carbon sequestration? *Geoderma*, **137**, 253–268.
- Jégou D, Cluzeau D, Hallaire V, Balesdent J, Tréhen P (2000) Burrowing activity of the earthworms *Lumbricus terrestris* and *Aporrectodea giardi* and consequences on C transfers in soil. *European Journal of Soil Biology*, **36**, 27–34.
- Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, **10**, 423–436.
- Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management*, **140**, 227–238.
- Johnson EA, Miyanishi K (2008) Testing the assumptions of chronosequences in succession. *Ecology Letters*, **11**, 419–431.
- Jug A, Makeschin F, Rehfuess KE, Hofmann-Schielle C (1999) Short-rotation plantations of balsam poplars, aspen and willows on former arable land in the Federal Republic of Germany. III. Soil ecological effects. *Forest Ecology and Management*, **121**, 85–99.
- Kaiser K, Guggenberger G (2003) Mineral surfaces and soil organic matter. European Journal of Soil Science, 54, 219–236.
- Kirschbaum MUF, Guo L, Gifford RM (2008) Observed and modelled soil carbon and nitrogen changes after planting
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a Pinus radiata stand onto former pasture. *Soil Biology & Biochemistry*, **40**, 247–257.

- Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review. *Journal of Plant Nutrition and Soil Science*, 163, 421–431.
- Lal R (2005) Forest soils and carbon sequestration. Forest Ecology and Management, 220, 242–258.
- Lemma B, Kleja DB, Nilsson I, Olsson M (2006) Soil carbon sequestration under different exotic tree species in the southwestern highlands of Ethiopia. *Geoderma*, **136**, 886–898.
- Lorenz K, Lal R (2005) The depth distribution of soil organic carbon in relation to land use and management and the potential of carbon sequestration in subsoil horizons. *Advances in Agronomy*, **88**, 35–66.
- Lugo AE, Brown S (1993) Management of tropical soils as sinks or sources of atmospheric carbon. *Plant and Soil*, **149**, 27–41.
- Mann LK (1986) Changes in soil carbon storage after cultivation. *Soil Science*, **142**, 279–288.
- Markewitz D, Sartori F, Craft C (2002) Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. *Ecological Applications*, **12**, 1276–1285.
- McKnight TL, Hess D (2007) *Physical Geography: A Landscape Appreciation*, 9th edn. Prentice Hall, Upper Saddle River, NJ.
- McLauchlan K (2006) The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. *Ecosystems*, **9**, 1364–1382.
- Mendham DS, O'Connell AM, Grove TS (2003) Change in soil carbon after land clearing or afforestation in highly weathered lateritic and sandy soils of south-western Australia. *Agriculture Ecosystems and Environment*, **95**, 143–156.
- Morris SJ, Bohm S, Haile-Mariam S, Paul EA (2007) Evaluation of carbon accrual in afforested agricultural soils. *Global Change Biology*, **13**, 1145–1156.
- Murty D, Kirschbaum MUF, McMurtrie RE, McGilvray A (2002) Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. *Global Change Biology*, **8**, 105–123.
- Ogle SM, Breidt FJ, Paustian K (2005) Agricultural management impacts on soil organic carbon storage under moist and dry climatic conditions of temperate and tropical regions. *Biogeochemistry*, **72**, 87–121.
- Parfitt RL, Percival HJ, Dahlgren RA, Hill LF (1997) Soil and solution chemistry under pasture and radiata pine in New Zealand. *Plant and Soil*, **191**, 279–290.
- Paul EA, Morris SJ, Six J, Paustian K, Gregorich EG (2003) Interpretation of soil carbon and nitrogen dynamics in agricultural and afforested soils. *Soil Science Society of America Journal*, 67, 1620–1628.
- Paul KI, Polglase PJ, Nyakuengama JG, Khanna PK (2002) Change in soil carbon following afforestation. *Forest Ecology* and Management, 168, 241–257.
- Paustian K, Collins HP, Paul EA (1997) Management controls on soil carbon. In: *Soil organic matter in temperate agroecosystems* (eds Paul EA, Elliott ET, Paustian K, Cole CV), pp. 15–49. CRC Press, Boca Raton, FL.
- Perrott KW, Ghani A, O'Connor MB, Waller JE (1999) Tree stocking effects on soil chemical and microbial properties at

the Tikitere Agroforestry Research Area. New Zealand Journal of Forestry Science, 29, 116–130.

- Pinno BD, Bélanger N (2008) Ecosystem carbon gains from afforestation in the Boreal Transition ecozone of Saskatchewan (Canada) are coupled with the devolution of Black Chernozems. *Agriculture Ecosystems and Environment*, **123**, 56–62.
- Post WM, Kwon KC (2000) Soil carbon sequestration and landuse change: processes and potential. *Global Change Biology*, 6, 317–327.
- Poulton PR, Pye E, Hargreaves PR, Jenkinson DS (2003) Accumulation of carbon and nitrogen by old arable land reverting to woodland. *Global Change Biology*, **9**, 942–955.
- Pregitzer KS, Palik BJ (1997) Changes in ecosystem carbon 46 years after establishing red pine (*Pinus resinosa* Ait.) on abandoned agricultural land in the Great Lakes Region. In: Soil Organic Matter Intemperate Agroecosystems: Long-Term Experiments in North America (eds Paul EA, Paustian KA, Elliott ET, Cole CV), pp. 263–270. CRC Press, Boca Raton, FL.
- Quideau SA, Bockheim JG (1996) Vegetation and cropping effects on pedogenic processes in a sandy prairie soil. *Soil Science Society of America Journal*, 60, 536–545.
- Resh SC, Binkley D, Parrotta JA (2002) Greater soil carbon sequestration under nitrogen-fixing trees compared with *Eucalyptus* species. *Ecosystems*, **5**, 217–231.
- Richter DD, Markewitz D, Trumbore SE, Wells CG (1999) Rapid accumulation and turnover of soil carbon in a re-establishing forest. *Nature*, 400, 56–58.
- Ritter E (2007) Carbon, nitrogen and phosphorus in volcanic soils following afforestation with native birch (*Betula pubescens*) and introduced larch (*Larix sibirica*) in Iceland. *Plant and Soil*, **295**, 239–251.
- Romanya J, Cortina J, Falloon P, Coleman K, Smith P (2000) Modelling changes in soil organic matter after planting fastgrowing *Pinus radiata* on Mediterranean agricultural soils. *European Journal of Soil Science*, **51**, 627–641.
- Ross DJ, Tate KR, Scott NA, Feltham CW (1999) Land-use change: effects on soil carbon, nitrogen and phosphorus pools and fluxes in three adjacent ecosystems. *Soil Biology and Biochemistry*, **31**, 803–813.
- Schiffman PM, Johnson WC (1989) Phytomass and detrital carbon storage during forest regrowth in the southeatern United States Piedmont. *Canadian Journal of Forest Research*, 19, 69–78.
- Scott NA, Tate KR, Ford-Robertson J, Giltrap DJ, Smith CT (1999) Soil carbon storage in plantation forests and pastures: land-use change implications. *Tellus Series B-Chemical and Physical Meteorology*, **51**, 326–335.
- Seely B, Welham C, Kimmins H (2002) Carbon sequestration in a boreal forest ecosystem: results from the ecosystem simulation model, FORECAST. *Forest Ecology and Management*, **169**, 123–135.
- Six J, Callewaert P, Lenders S *et al.* (2002a) Measuring and understanding carbon storage in afforested soils by physical fractionation. *Soil Science Society of America Journal*, 66, 1981–1987.
- Six J, Conant RT, Paul EA, Paustian K (2002b) Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant and Soil*, **241**, 155–176.

- Six J, Elliott T, Paustian K (1999) Aggregate and soil organic matter dynamics under conventional and no-tillage systems. *Soil Science Society of America Journal*, 63, 1350–1358.
- Six J, Elliott ET, Paustian K (2000) Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture. *Soil Biology and Biochemistry*, 32, 2099–2103.
- Skjemstad JO, Krull ES, Swift RS, Szarvas S (2008) Mechanisms of protection of soil organic matter under pasture following clearing of rainforest on an Oxisol. *Geoderma*, 143, 231–242.
- Smal H, Olszewska M (2008) The effect of afforestation with Scots pine (*Pinus silvestris* L.) of sandy post-arable soils on their selected properties. II. Reaction, carbon, nitrogen and phosphorus. *Plant and Soil*, **305**, 171–187.
- Smith P (2004) How long before a change in soil organic carbon can be detected? *Global Change Biology*, **10**, 1878–1883.
- Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma*, 74, 65–105.
- Strong WL, La Roi GH (1983) Root-system morphology of common boreal forest trees in Alberta, Canada. Canadian Journal of Forest Research, 13, 1164–1173.
- Turner J, Lambert M (2000) Change in organic carbon in forest plantation soils in eastern Australia. *Forest Ecology and Management*, **133**, 231–247.
- Turner J, Lambert MJ, Johnson DW (2005) Experience with patterns of change in soil carbon resulting from forest plantation establishment in eastern Australia. *Forest Ecology and Management*, 220, 259–269.
- VandenBygaart AJ, Angers DA (2006) Towards accurate measurements of soil organic carbon stock change in agroecosystems. *Canadian Journal of Soil Science*, 86, 465–471.

- Vesterdal L, Ritter E, Gundersen P (2002) Change in soil organic carbon following afforestation of former arable land. *Forest Ecology and Management*, **169**, 137–147.
- Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P (2008) Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management*, **255**, 35–48.
- von Lutzow M, Kogel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner B, Flessa H (2006) Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions a review. *European Journal of Soil Science*, **57**, 426–445.
- Wang CM, Ouyang H, Shao B, Tian Y-Q, Zhao J-G, Xu H-Y (2006) Soil carbon changes following afforestation with olga bay larch (*Lariz olgensis* Henry) in Northeastern China. *Journal of Inte*grative Plant Biology, 48, 503–512.
- Yakimenko EY (1998) Soil comparative evolution under grasslands and woodlands in the forest zone of Russia. In: *Management of carbon sequestration in soil* (eds Lal R, Kimble JM, Follett RF, Stewart BA), pp. 391–404. CRC Press, Boca Raton, FL.
- Zerva A, Mencuccini M (2005) Carbon stock changes in a peaty gley soil profile after afforestation with Sitka spruce (*Picea sitchensis*). *Annals of Forest Science*, **62**, 873–880.
- Zinn YL, Resck DVS, da Silva JE (2002) Soil organic carbon as affected by afforestation with *Eucalyptus* and *Pinus* in the Cerrado region of Brazil. *Forest Ecology and Management*, **166**, 285–294.
- Zou X, Bashkin M (1998) Soil carbon accretion and earthworm recovery following revegetation in abandoned sugarcane fields. *Soil Biology and Biochemistry*, **30**, 825–830.