



## *Tansley review*

# The likely impact of elevated [CO<sub>2</sub>], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review

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## Summary

**Key words:** carbon balance, carbon dioxide (CO<sub>2</sub>), climate change, fertilization, global warming.

Temperate and boreal forest ecosystems contain a large part of the carbon stored on land, in the form of both biomass and soil organic matter. Increasing atmospheric [CO<sub>2</sub>], increasing temperature, elevated nitrogen deposition and intensified management will change this C store. Well documented single-factor responses of net primary production are: higher photosynthetic rate (the main [CO<sub>2</sub>] response); increasing length of growing season (the main temperature response); and higher leaf-area index (the main N deposition and partly [CO<sub>2</sub>] response). Soil organic matter will increase with increasing litter input, although priming may decrease the soil C stock initially, but litter quality effects should be minimal (response to [CO<sub>2</sub>], N deposition, and temperature); will decrease because of increasing temperature; and will increase because of retardation of decomposition with N deposition, although the rate of decomposition of high-quality litter can be increased and that of low-quality litter decreased. Single-factor responses can be misleading because of interactions between factors, in particular those between N and other factors, and indirect effects such as increased N availability from temperature-induced decomposition. In the long term the strength of feedbacks, for example the increasing demand for N from increased growth, will dominate over short-term responses to single factors. However, management has considerable potential for controlling the C store.

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## I. Introduction

Forest ecosystems contain a large part of the carbon stored on land, in the form of both biomass and soil organic matter (SOM). The long-term fate of C in forest ecosystems depends on whether it is stored in living biomass or soils. Forest trees also control the major terrestrial bidirectional transfer of C between the atmosphere and the soil: forests take up large amounts of CO<sub>2</sub> from the atmosphere through photosynthesis, and return large amounts through respiration by vegetation and decomposers in the soil. Carbon stocks in soil exceed those in vegetation by *c.* 2 : 1 in northern temperate forests to over 5 : 1 in boreal forests (Dixon *et al.*, 1994; Schlesinger, 1997). Thus changes in soil C stocks can be more important than changes in vegetation C stocks for forest C budgets (Medlyn *et al.*, 2005). Increasing atmospheric carbon dioxide concentration [CO<sub>2</sub>] with subsequent changing climate, increased nitrogen deposition, and changing land use have changed (and will change) the forest C stocks.

Over the past 200 yr, approx. 405 ± 30 Pg C has been emitted into the atmosphere as CO<sub>2</sub> as a result of fossil fuel burning and cement production (75%), and of land use and land-use change (25%), predominantly deforestation (IPCC, 2001). As a result, the global average atmospheric [CO<sub>2</sub>] has risen by approx. 35%, from 280 ± 5 to 377 ppmv, in 2004 (WMO, 2006). This increase in [CO<sub>2</sub>] accounts for approx. 40% of these anthropogenic emissions, the remainder having

been absorbed by the oceans and terrestrial ecosystems. On average during the 1990s, annual global emissions of greenhouse gases amounted to 6.4 ± 0.3 Pg C from fossil fuels, plus 1.7 ± 0.8 Pg C from land use and land-use change, mainly deforestation in the tropics. There are four main global sinks for these emissions: the atmosphere (3.2 ± 0.1 Pg C); the oceans (1.7 ± 0.5 Pg C); tropical vegetation (1.9 ± 1.3 Pg C); and temperate and boreal vegetation, mainly forests (1.3 ± 0.9 Pg C) (Read *et al.*, 2001). In particular, plant photosynthesis is responding to this increase in [CO<sub>2</sub>].

Deposition of N – wet and dry, oxidized and reduced – to forests is between 1 and 100 kg ha<sup>-1</sup> yr<sup>-1</sup>. The smaller amounts occur in the more remote forests, particularly in rural areas at high latitudes; the large amounts in industrialized central Europe (Jarvis & Fowler, 2001). Part of the N delivered to forests in this way is absorbed directly by the leaves and needles of trees without reaching the ground, and fine roots, mycorrhizae and decomposer organisms quickly scavenge the N that does reach the ground. A key uncertainty is to what extent, and for how long, high annual rates of N deposition will be able to stimulate the production of mature forests, and whether detrimental effects such as N saturation will eventually appear (Aber *et al.*, 1989, 1998; Binkley & Högborg, 1997).

The average global temperature increased during the 20th century by 0.6°C, and projections are for an additional increase of 1.4–5.8°C during the 21st century (IPCC, 2001). The likely effects of temperature extend from straightforward,

direct effects on biochemical reactions to indirect effects through lengthening growing seasons (Myneni *et al.*, 1997), with potential risks of passing temperature thresholds to particular responses.

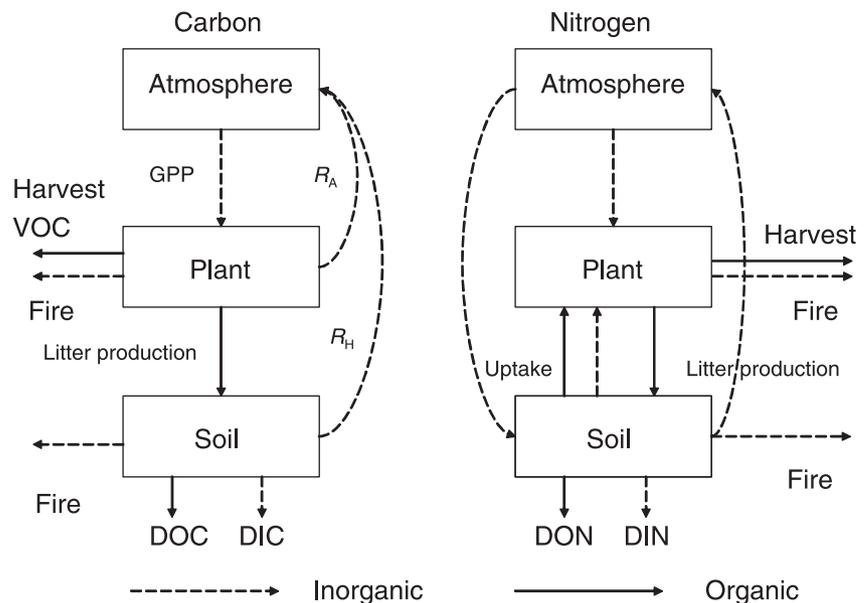
Forests in the northern hemisphere are in a transient state of development when considered on both long and short time scales. At mid-to-high latitudes, the forests present today have been migrating, evolving and developing since the ice retreated after the last glaciation. Large amounts of C have accumulated in these forests over the past 10 000 yr, and are continuing to accumulate in many forests. In central Europe there has been a long history of forest exploitation and management, so that many of today's forests were relatively recently established in the 18th century. In North America, particularly in the north-east, land was cleared for agriculture in the 17th and 18th centuries, but was abandoned to forest regrowth (so-called 'old field succession') in the 19th century as farmers moved westwards. Elsewhere, areas of forest are recovering from naturally occurring fires caused by lightning strikes and windthrow resulting from severe storms.

The global increase in [CO<sub>2</sub>], temperature and N that has occurred so far has also probably contributed to the current C sinks in forests of the north temperate and boreal regions. In particular, N has been identified as a driving factor in

European forests (Binkley & Högberg, 1997; Karjalainen *et al.*, in press). A stand of trees is a C sink if the uptake of CO<sub>2</sub> in gross photosynthesis (gross photosynthetic production, GPP) exceeds the losses of CO<sub>2</sub> in total ecosystem respiration ( $R_E = R_A + R_H$ ) and volatile organic compounds (Fig. 1). In general, a stand has the potential to be a C sink in daytime, a C source at night, a C sink in summer, and a C source in winter. Stands will also be sinks or sources of varying strength, depending on their stage in the life cycle of trees and the management cycle of forest stands.

Mature and over-mature forests are of particular concern with respect to the long-term permanence of forest C sinks. On the basis of the 'climax concept' (Clements, 1916), it has long been believed that largely undisturbed, old-growth forests are in a state of equilibrium, such that over a period of years they are C-neutral, with neither net gain nor loss of C. This view has been challenged in recent years with increasing evidence from long-term measurements of tree growth on sample plots and measurements of CO<sub>2</sub> fluxes in old-growth stands that indicate widespread increases in growth and net primary production (NPP) of stands across Europe (Spiecker *et al.*, 1996) and in the neotropics (Malhi *et al.*, 2004). There are several possible explanations as to why natural and seminatural mature stands and old-growth forests are C sinks

**Fig. 1** Gross primary production (GPP) is the uptake of carbon in photosynthesis by foliage of trees in the forest from the atmosphere. Carbon losses as a result of autotrophic respiration ( $R_A$ ) and loss of volatile organic C (VOC) from the foliage reduce this uptake to net primary production (NPP). At the scale of the stand, further C losses occur because of heterotrophic respiration ( $R_H$ ) associated with decomposition of dead organic matter, resulting in the net ecosystem exchange (NEE). Additional losses of dissolved inorganic C (DIC) and dissolved organic C (DOC) in drainage through the soil profile into rivers and into the atmosphere reduce this amount to the net ecosystem production (NEP). Finally, at the scale of the forest and landscape, losses caused by disturbances ( $D$ ), such as fire, herbivory and management activities, further reduce the amount of C stored in the forest. The resulting net imbalance of the forest ecosystem can be interpreted as the net biome productivity (NBP). The nitrogen cycle parallels the C cycle, but has an additional flux through uptake of N from the soil. Note: Chapin *et al.* (2006) recently suggested the use of somewhat different, and more consistent, terms related to carbon cycling. A change to their terminology would, however, not alter the conclusions in the present paper.



$NPP = GPP - R_A - VOC$	$NPP \equiv \text{Litter production}$
$NEE = NPP - R_H$	$R_E = R_A + R_H$
$F_c = GPP - R_E$	
$NEP = NEE - DIC - DOC$	
$NBP = NEP - D$	

today, a likely driving force being the human-induced changes in the atmosphere that have occurred over the past one and a half centuries.

In this review we address C storage in northern forests as affected by (1) accumulation of C in managed forests between major disturbances; (2) recovery and management of C stocks; (3) permanence of C stocks – the climax concept vs increase in growth of old-growth stands; and (4) impacts on C stocks of  $[\text{CO}_2]$ , N and temperature. This review updates earlier reviews (Ceulemans & Mousseau, 1994; Saxe *et al.*, 1998, 2001; Poorter & Navas, 2003; Nowak *et al.*, 2004; Ainsworth & Long, 2005), takes an ecosystem perspective, and emphasizes interactions between individual factors and management options.

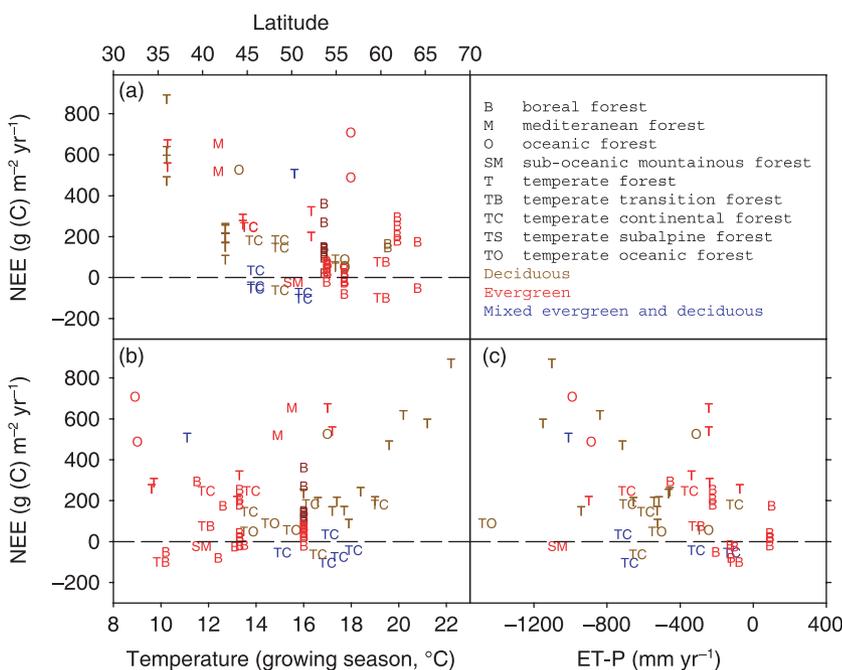
## II. Net ecosystem exchange and changes in carbon stocks

Changes in the total C stocks in forest stands (net ecosystem exchange, NEE) can be assessed by summing the changes in both vegetation and soil (Fig. 1). Changes in tree C stocks over a 5-yr period (the length of the Kyoto commitment period) can be assessed with reasonable precision by standard inventory methods, such as those used in national forest inventories (Gower *et al.*, 2001). Changes in soil C stocks can also be determined by standard sampling techniques, but very many samples are required to achieve adequate precision over a period as short as 5 yr (Conen *et al.*, 2003, 2005; Smith, 2004). Another way to estimate annual C balances is to measure biomass accumulation, net photosynthesis, and the autotrophic and heterotrophic respiration fluxes. This usually involves integrating and scaling up point measurements in

space and time, with a relatively large uncertainty in the final, annual storage term because of the many assumptions involved (Malhi *et al.*, 1999).

Alternatively, the net turbulent flux of  $\text{CO}_2$  over a canopy can be determined by eddy-covariance measurements, and may be extrapolated to the overall net  $\text{CO}_2$  exchange, over periods of hours to years (Aubinet *et al.*, 2000). According to definitions illustrated in Fig. 1, eddy-covariance measurements of  $\text{CO}_2$  net flux,  $F_c$ , may not be interpreted strictly as NEE, but correspond to the difference between GPP and ecosystem respiration ( $R_E$ ). This may be important as C is also exchanged in the gas phase by forest ecosystems as non $\text{CO}_2$  organic forms such as isoprene and methane (Harley *et al.*, 1997). The accuracy of eddy-covariance measurements used under ideal site conditions is believed to be  $\pm 50 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Baldocchi, 2003). Spatial variation originating from underlying variability in ecosystem attributes (e.g. leaf-area index, LAI) may, however, result in coefficients of variation (SD relative to the mean) of 10%, even over very uniform forests (Oren *et al.*, 2006). Recent measurements made on >100 young and mature forest stands worldwide, with a range of species and management histories, have yielded annual values of  $\text{CO}_2$  exchange from approx.  $-100$  to  $250 \text{ g C m}^{-2} \text{ yr}^{-1}$  for boreal forests; from  $250$  to  $700 \text{ g C m}^{-2} \text{ yr}^{-1}$  for temperate forests; and from  $100$  to  $600 \text{ g C m}^{-2} \text{ yr}^{-1}$  for humid tropical forests (Malhi *et al.*, 1999). (We are using the sign convention that NEE is positive when the forest is taking up  $\text{CO}_2$ .)

Net ecosystem exchange from eddy-covariance measurements shows a decreasing trend with latitude (Fig. 2a). The forest stands in the temperate region tend to be stronger C sinks than the boreal forest stands, although the boreal evergreen



**Fig. 2** Net ecosystem exchange (NEE) as a function of (a) latitude, (b) growing-season temperature and (c) humidity index (evapotranspiration minus precipitation) (from Black *et al.*, 2005). The same site may be represented by data from more than 1 yr.

conifer stand in an oceanic climate is a sink comparable with the best of the temperate forest stands. Growing-season length, temperature and humidity index appear to be the important variables determining the potential size of the C sink (Fig. 2b,c). Measurements of NEE made over several years on boreal forest stands have shown major variations in the annual amount of C sequestered, depending largely on when the thaw occurred. A thaw occurring 2 wk earlier than usual may lead to an additional annual sequestration of  $100 \text{ g C m}^{-2}$  (Black *et al.*, 2005). Under the same temperature regime, evergreen stands tend to be stronger sinks than stands of deciduous trees.

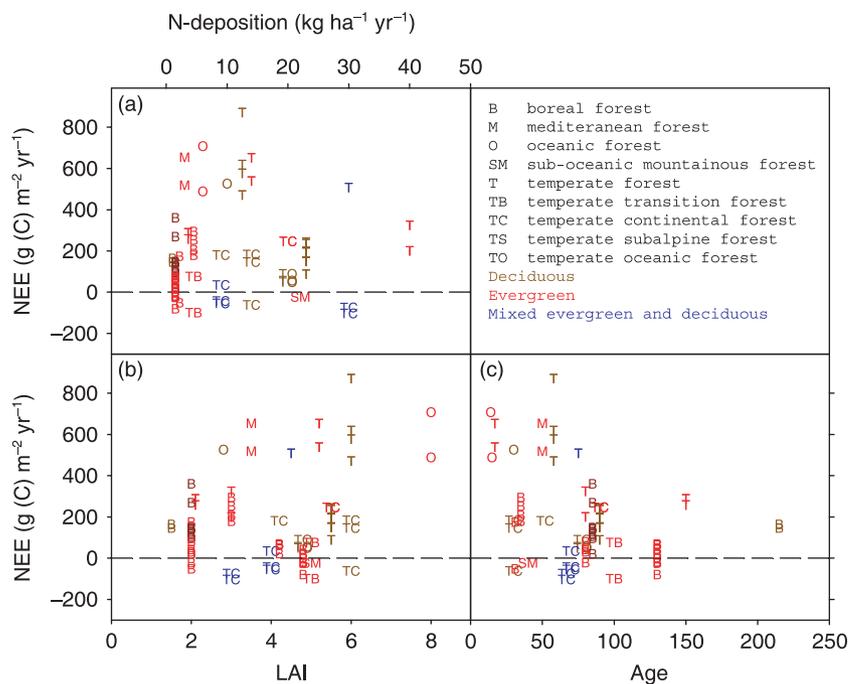
Eddy-covariance measurements show, in general, that young forest stands (<25 yr old) are stronger C sinks than old stands (Fig. 3c). Data collected over chronosequences in managed European forests demonstrate that NEE peaks at an age varying from 10 to 60 yr and generally declines thereafter. This pattern is consistent with the results obtained in a fire chronosequence in a temperate dry forest in North America (Law *et al.*, 2003). Although NEE clearly can be maintained without significant decline beyond 60 yr (Lloyd *et al.*, 2002), NEE has been found to reach neutral status in some old-growth boreal forests (Law *et al.*, 2003; Carrara *et al.*, 2004; Kolari *et al.*, 2004). Some of the stands in Fig. 3c, particularly the older ones, are close to C-neutral or are C sources, and there are other observations of old-growth stands close to a neutral C balance (Goulden *et al.*, 1998; Lindroth *et al.*, 1998; Valentini *et al.*, 2000; Janssens *et al.*, 2001; Carrara *et al.*, 2004; Pregitzer & Euskirchen, 2004), although 100-yr-old oak–hickory forest can be as strong a sink as a fast-growing young *Pinus taeda* plantation (Stoy *et al.*, 2006), and Siberian *Pinus sylvestris*

forests continued to be C sinks even at an age of 200 yr (Schulze *et al.*, 1999). The age-related trend in NEE still appears to be poorly documented for the postmature stage, and firm conclusions cannot be drawn so far from the present data.

If we take a relatively short-term snapshot, it is reasonable to assume that undisturbed forests would, over decades, have C balances that are close to equilibrium ( $NEE \approx 0$ ). Disturbance will remove a forest from equilibrium; the major questions are how rapidly, and by which routes, a disturbed forest will adjust to a new equilibrium. In the short term, the key question is how net canopy photosynthesis ( $P$ ) and decomposition are influenced by temperature ( $T$ ),  $[\text{CO}_2]$  and N, because biomass production and C sequestration are closely connected, and the latter depends on the balance between C uptake through  $P$  and release through decomposition.  $P$  is a function of  $T$ ,  $[\text{CO}_2]$  ( $C_a$ ), availability of water ( $W$ ), availability of N ( $N_a$ ), absorbed solar radiation ( $Q$ ), and foliage leaf-area index ( $L$ ):

$$P = f(T, C_a, W) \times f(N_a) \times f(Q, L)$$

In a three-pool model,  $P$  responds rapidly to  $C_a$  and  $N_a$ . Litter production responds somewhat more slowly, and heterotrophic respiration yet more slowly because the latter can only increase after the build-up of a larger SOM pool. The effect of  $T$  is mainly through an initial increase in the specific rate of heterotrophic respiration (shorter residence time of soil C), which eventually declines towards the previous rate when the labile soil C pool has declined. Other single-factor effects on C fluxes will also follow the same qualitative patterns. For example,  $P$  will respond to  $T$  and heterotrophic respiration to



**Fig. 3** Net ecosystem exchange (NEE) as a function of (a) nitrogen deposition, (b) leaf-area index (LAI) and (c) stand age (from Black *et al.*, 2005). The same site may be represented by data from more than 1 yr.

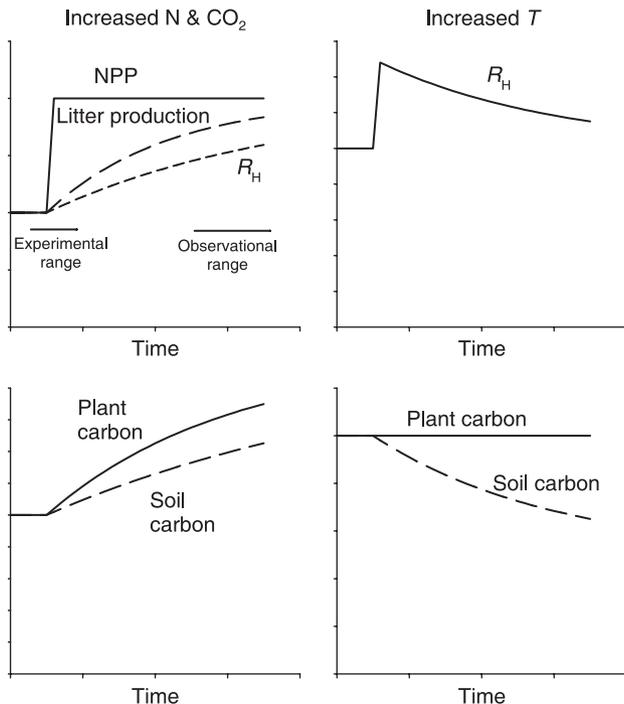
$N_a$  (Fig. 4). Conceptually, the effects of increased  $T$ , elevated  $[CO_2]$  and increased N deposition in unmanaged and managed forests can be analysed one at a time with changes in pool size determined by turnover rates of those pools

(Fig. 4; Goudriaan, 1990). The following sections expand the single factor responses in more detail and develop chains of responses, with a summary in Table 1.

### III. Elevated $[CO_2]$

#### 1. Plant carbon

Hundreds of experiments have shown that increasing  $[CO_2]$  stimulates tree growth, and the results from short-term studies with seedlings, field studies with saplings, and longer-term, whole-stand manipulations have been reviewed previously (Ceulemans & Mousseau, 1994; Curtis & Wang, 1998; Norby *et al.*, 1999; Gielen & Ceulemans, 2001; Medlyn *et al.*, 2001; Norby *et al.*, 2005). The growth enhancement from  $CO_2$  enrichment generally occurs through increases in the rates of net photosynthesis in the order of 40–80% (Saxe *et al.*, 1998; Medlyn *et al.*, 1999), compounded by an increase in leaf area. Observed long-term increases in net photosynthesis are typically somewhat lower than the short-term response. The downward acclimation with time of photosynthesis appears to be related primarily to dilution of the leaf N concentration (Ellsworth *et al.*, 2004). The growth response to elevated  $[CO_2]$  of young trees with expanding canopies is often further enhanced by increased leaf production, leading to larger LAI (Ainsworth & Long, 2005). Similarly, the leaf area of individual trees growing in a sparse stand with low LAI increased by nearly 22% with increasing  $[CO_2]$  alone (Kellomäki & Wang, 1997). Increasing  $[CO_2]$  and temperature resulted in only about half as much increase in LAI, with temperature alone having no effect.



**Fig. 4** Qualitative responses of net primary production (NPP), litterfall, heterotrophic respiration ( $R_H$ ), and plant and soil carbon pools to step changes in  $[CO_2]$ , nitrogen and temperature ( $T$ ).

**Table 1** Important cause–effect chains for carbon cycling

No.	Rate*	Perturbation	Cause–effect chain	Strength†	Knowledge‡
1	Fast	$[CO_2] \uparrow$	$NPP \uparrow \Rightarrow N \text{ demand} \uparrow \Rightarrow \text{Soil N availability} \downarrow \Rightarrow NPP \downarrow$	Strong	High
2	Fast	$N \uparrow$	$NPP \uparrow$	Strong	High
3	Fast	$T \uparrow$	$NPP \uparrow \Rightarrow N \text{ demand} \uparrow \Rightarrow \text{Soil N availability} \downarrow \Rightarrow NPP \downarrow$	Strong	High
4	Fast	$T \uparrow$	$\text{Soil respiration} \uparrow \Rightarrow \text{Soil carbon} \downarrow \Rightarrow \text{Soil respiration} \downarrow$	Strong	High
5	Fast	$[CO_2] \uparrow$	$\text{Allocation to roots and mycorrhiza} \uparrow \Rightarrow \text{Soil respiration} \uparrow$	Medium	High
6	Fast	$T \uparrow$	$\text{Turnover of fine roots} \downarrow \Rightarrow ?$	Medium	Medium
7	Intermediate	$T \uparrow$	$N \text{ mineralization} \uparrow \Rightarrow NPP \uparrow \Rightarrow \text{See mechanisms above}$	Strong	High
8	Intermediate	$N \uparrow$	$\text{Root allocation} \downarrow \Rightarrow \text{Root litter} \downarrow \Rightarrow \text{Soil C store} \downarrow$	Medium	Medium
9	Intermediate	$N \uparrow$	$\text{Mycorrhizal turnover} \uparrow \Rightarrow \text{Litter input in soil} \uparrow \Rightarrow \text{Soil C store} \uparrow$	Weak	Weak
10	Intermediate	$N \uparrow$	$\text{Litter N concentration} \uparrow \Rightarrow \text{Litter decomposition rate} \uparrow \Rightarrow \text{Soil C store} \downarrow$	Weak	Unclear
11	Intermediate	$[CO_2] \uparrow$	$\text{Litter N concentration} \downarrow \Rightarrow \text{Litter decomposition rate} \downarrow \Rightarrow \text{Soil C store} \uparrow$	Weak	Unclear
12	Intermediate	$N \uparrow, [CO_2] \uparrow$	$NPP \uparrow \Rightarrow \text{Litter production} \uparrow \Rightarrow \text{SOM} \uparrow$	Weak	High
13	Intermediate	$N \uparrow$	$NPP \uparrow \text{ and root allocation} \downarrow \Rightarrow N \text{ uptake} \downarrow \Rightarrow NPP \downarrow$	Medium	Medium
14	Intermediate	$[CO_2] \uparrow$	$NPP \uparrow \text{ and root allocation} \uparrow \Rightarrow N \text{ uptake} \uparrow \Rightarrow NPP \uparrow$	Medium	Medium
15	Intermediate	$N \uparrow$	$\text{Soil respiration} \downarrow \Rightarrow N \text{ mineralization} \downarrow \Rightarrow NPP \downarrow$	Medium	Weak
16	Intermediate	$N \uparrow$	$\text{Litter decomposition rate} \uparrow \Rightarrow \text{Soil C store} \downarrow$	Medium	Weak
17	Slow	$N \uparrow$	$\text{SOM decomposition rate} \downarrow \Rightarrow \text{Soil C store} \uparrow$	Medium	Weak

\*Rate at which cause–effect chains respond: fast, within-year; intermediate, a few years; slow, decades; very slow, centuries.

†Strength of the effects.

‡Knowledge of the links in the chain.

NPP, net primary production; SOM, soil organic matter.

Large, mature forest trees respond physiologically to elevated  $[\text{CO}_2]$  in a manner similar to the younger trees used in most studies (Körner *et al.*, 2005). In closed-canopy stands, the increase in NPP can, however, result from both increase in leaf area and light absorption at low LAI, and increased light-use efficiency at high LAI (Norby *et al.*, 2005). For instance, LAI was not found to increase with elevated  $[\text{CO}_2]$  in dense temperate forest plantations (Sigurdsson *et al.*, 2001; Norby *et al.*, 2003), whereas in young, aggrading forests, leaf area has been found to increase quite rapidly. However, recent analyses of free-air  $\text{CO}_2$  enrichment (FACE) data show that with increasing soil nutrient supply, stands under elevated  $[\text{CO}_2]$  diverge in LAI from stands under ambient  $[\text{CO}_2]$ , even in dense stands, with the aboveground NPP increasing with LAI, without additional effects of elevated  $[\text{CO}_2]$  (McCarthy *et al.*, 2006; Palmroth *et al.*, 2006).

Questions remain as to whether the stimulation by elevated  $[\text{CO}_2]$  will persist over many decades, particularly if sink activity is limited by nutrient availability (Sigurdsson *et al.*, 2001; Körner, 2003, 2006; van Groenigen *et al.*, 2006), or if N is progressively sequestered in SOM and is no longer available (Luo *et al.*, 2004). So far, however, increasing  $[\text{CO}_2]$  has not been found either to stimulate N mineralization (Finzi *et al.*, 2002) or to slow down N availability (Zak *et al.*, 2003).

Respiration is also affected by  $[\text{CO}_2]$ . In a FACE study of a *Liquidambar styraciflua* stand at Oak Ridge, TN, USA, upper canopy leaves in elevated  $[\text{CO}_2]$  had significantly larger numbers of mitochondria, leaf mass per unit area and leaf starch than did lower canopy leaves, resulting in higher night-time respiration rates (Tissue *et al.*, 2002). Stem respiration was increased by 33% in elevated  $[\text{CO}_2]$ ; the increase was driven by increased substrate supply from the leaves (Edwards *et al.*, 2002). Similar results have been reported from experiments with *Populus* spp., in which effects of elevated  $[\text{CO}_2]$  were modified by crown architecture or by leaf or growth phenology (Sigurdsson, 2001; Gielen *et al.*, 2002). From a FACE experiment with *P. taeda*, Hamilton *et al.* (2001) concluded that elevated  $[\text{CO}_2]$  had little direct effect on leaf tissue respiration, and that the influence of elevated  $[\text{CO}_2]$  on respiration was primarily through increased biomass.

The allocation of C to stem biomass or to fast-turnover pools has important implications for the capacity of the forest to retain the assimilated C. Carbon that is allocated to woody biomass will persist in the ecosystem for many years, whereas C allocated to fine roots, which turn over rapidly, may not. Nutrient-limited trees growing in elevated  $[\text{CO}_2]$  have been shown to increase allocation towards belowground sinks for assimilate (Linder & Murray, 1998; Oren *et al.*, 2001; Butnor *et al.*, 2003; Palmroth *et al.*, 2006), and may senesce or drop their leaves earlier (Sigurdsson, 2001). King *et al.* (2001) observed a 96% increase in fine-root biomass in a mixed stand of trembling aspen and paper birch, and higher proportions of C can be found to be allocated below ground (Janssens *et al.*, 2005), although this does not appear to be the case universally

(Tingey *et al.*, 2000). The increased production does not always result in larger standing root biomass, as root turnover can also increase (Phillips *et al.*, 2006). A strong interaction between  $[\text{CO}_2]$  and N is observed in many experiments such that root-growth responses are obtained only at high N levels (Prior *et al.*, 1997; Kasurinen *et al.*, 1999; Pregitzer *et al.*, 2000; Zak *et al.*, 2000). However, fine-root production more than doubled under elevated  $[\text{CO}_2]$  in an N-limited *L. styraciflua* forest (Norby *et al.*, 2004). Although annual fine-root mortality matched production, standing crop was significantly greater in elevated  $[\text{CO}_2]$  in midsummer, and the increased presence of fine roots was related to increased N uptake (Norby *et al.*, 2004).

It is possible that  $[\text{CO}_2]$  effects are mediated mostly through LAI. The fraction of aboveground NPP allocated to wood, a relatively slow turnover pool, increased with LAI in broadleaf FACE experiments (approx. 50% at low LAI, reaching a maximum of 70% at moderate LAI), with the effect of elevated  $[\text{CO}_2]$  on allocation accounted for entirely by changes in LAI. In pines, allocation to wood decreased with increasing LAI (from approx. 65 to 55%), but is higher (approx. 68–58%) under elevated  $[\text{CO}_2]$  at any LAI level (McCarthy *et al.*, 2006). Total belowground C allocation, most of which returns to the atmosphere as  $\text{CO}_2$  efflux from the soil, decreased with increasing LAI, reflecting increasing strength of the aboveground sink for C, but the enhancement under elevated  $[\text{CO}_2]$  was constant (approx. 22%) over the entire range of LAI; the response was consistent regardless of the cause of the change in LAI, including increases in LAI with N addition and decreases with droughts (Oren *et al.*, 2001; Palmroth *et al.*, 2006).

The above discussion does not take into account the site-specific balance between water availability and demand, dependent on both soil hydrology and atmospheric conditions. Allocation of the additional carbohydrates generated in elevated  $[\text{CO}_2]$  must reflect this balance in such a way that the root surface area for water uptake is matched with the transpiring leaf surface area, with hydraulic design adjusted accordingly (Hacke *et al.*, 2001). At sites with limited water availability, more carbohydrates allowing the production of a larger leaf biomass and surface area may necessitate increased allocation of biomass to roots below ground, so as to maintain a correspondingly larger standing fine-root biomass (Ewers *et al.*, 2000, 2001).

## 2. Soil carbon

To date, most studies on the effects of elevated  $[\text{CO}_2]$  have focused on litter properties, and few studies have been made on soil organic C (SOC) stocks in forest ecosystems. Further, the results refer to periods shorter than a decade, often not long enough to fully appreciate SOC changes. Elevated  $[\text{CO}_2]$  is expected to produce energy-rich but nutrient-poor litter, for example, higher C : N ratios (van de Geijn & van Veen, 1993). In a meta-analysis of data from senescent leaves,

Norby *et al.* (2001) found an average N reduction of 7.1% and an increase in lignin of 6.5% in leaves of plants grown in elevated  $[\text{CO}_2]$  compared with those grown in ambient  $[\text{CO}_2]$ . Additionally, plant tissues grown in elevated  $[\text{CO}_2]$  have decreased N concentrations (Cotrufo *et al.*, 1998a; Norby *et al.*, 1999); changes in the composition and concentration of tannins and phenolics (Kainulainen *et al.*, 1998); and modification of physical structure with thicker leaves (Radoglou & Jarvis, 1990a, 1990b; Taylor *et al.*, 2004). On the basis of such observations, the hypothesis arose that plant tissues grown in elevated  $[\text{CO}_2]$  would decompose more slowly than leaves grown in ambient  $[\text{CO}_2]$ , with negative feedbacks on N cycling and, in turn, on plant growth enhancement by elevated  $[\text{CO}_2]$  (Strain & Bazzaz, 1983). A comprehensive review showed that leaves grown in elevated  $[\text{CO}_2]$  did not reduce litter decomposition rates significantly (Norby *et al.*, 2001). Growth in elevated  $[\text{CO}_2]$  may, however, affect decomposition by changing the amount and dynamics of litter fall (Schlesinger & Lichter, 2001); by modifying litter quality through changes in plant community composition; and by altering the soil environment and its biological activity (by increase of soil water, C input to soil, rhizosphere activity, etc.). These indirect effects can be tested only by long-term studies on litter decomposition in forests exposed to elevated  $[\text{CO}_2]$ , but the current literature comprises results only from short-term incubations (Finzi & Schlesinger, 2002; Cotrufo *et al.*, 2005). Decomposition of root litter has received much less attention, but given the aforementioned increase in fine-root production that often occurs in response to elevated  $[\text{CO}_2]$ , the fate of dead roots may be especially important for soil C dynamics. In some cases, elevated  $[\text{CO}_2]$  has promoted root production deeper in the soil profile (Norby *et al.*, 2004; Johnson *et al.*, 2006), where decomposition may be slower.

Hoosbeek *et al.* (2004) reported a decreased C stock in soils exposed to elevated  $[\text{CO}_2]$  at the end of a 3-yr rotation of a poplar plantation. This change occurred despite larger litter inputs, and was attributed to priming of decomposition of the native SOC. When the study was continued for an additional 2 yr there was, however, a faster increase of SOC in the mineral soil under elevated  $[\text{CO}_2]$  (Hoosbeek *et al.*, 2006). Similarly, the SOC content had increased significantly in a sweetgum (*L. styraciflua*) plantation after 5 yr of FACE (Jastrow *et al.*, 2005). In the loblolly pine (*P. taeda*) forest at the Duke University FACE experiment, a build-up of litter on the forest floor occurred in the FACE rings (Schlesinger & Lichter, 2001); this was, however, interpreted as a transient response that would not ultimately lead to significant, long-term C accumulation. In a review of 56 observations of C in mineral soils, mostly from elevated  $\text{CO}_2$  crop experiments, van Groenigen *et al.* (2006) noted that unless more than  $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  was added as fertilizer, SOC did not change. Jastrow *et al.* (2005), however, concluded that although most experiments have been unable individually to document a response of soil C to elevated  $\text{CO}_2$ , meta-analysis indicated

that collectively, in outdoor experimental studies lasting at least 2 yr (including forests, grasslands and chaparral), soil C increased by 5.6%, corresponding to an accrual rate of  $19 \text{ g C m}^{-2} \text{ yr}^{-1}$ . This conclusion is consistent with the premise that parts of the additional litter produced under elevated  $\text{CO}_2$  will eventually enter the SOM in the form of coarse particulate organic matter, where it will initiate aggregate formation and promote C sequestration (Six *et al.*, 1998). This process may contribute to an increase of soil C stocks in the long term.

## IV. Temperature

### 1. Plant carbon

Air-warming experiments have shown a positive single-factor effect of temperature on photosynthetic rate (Kellomäki & Wang, 1996), but temperature and  $[\text{CO}_2]$  frequently interact. Photosynthetic rate increases substantially with  $[\text{CO}_2]$  and the effect is more pronounced at temperatures around  $20^\circ\text{C}$  than at  $10^\circ\text{C}$  (Sigurdsson *et al.*, 2002). Taken together, the expected atmospheric changes are likely to stimulate the photosynthetic rate at the leaf scale; but at the stand scale, increasing leaf area may diminish these gains as a result of increased respiratory costs associated with partial shading of more leaf area (Oren *et al.*, 1986). Acclimation of the photosynthetic and respiratory processes may also be important (Atkin & Tjoelker, 2003). Whether or not an increase in canopy leaf area increases C gain depends on the pre-existing canopy leaf area and the canopy structure. Canopies with second- and third-order grouping of the foliage can obtain photosynthetic benefit from an increase in leaf area when this would not eventuate with a random leaf area distribution (Wang & Jarvis, 1991).

Results from a Swedish soil-warming study (Bergh & Linder, 1999) led Majdi & Öhrvik (2004) to suggest that fine-root production was a function of the length of the growing season, and that root mortality increased as soil temperature rose, resulting in a higher C-turnover rate. Future increases in temperature may also increase root mortality more in N-rich soils in temperate forests than in N-poor soils in boreal forests. On suitable sites (e.g. sites with deep, underexploited soils), some of the additional carbohydrates may be allocated to the production of fine roots (Norby *et al.*, 2004) and to mycorrhizal biomass, and the rest may cycle rapidly back to the atmosphere (Schäfer *et al.*, 2003). This rapid cycling may reflect increased rhizodeposition of excess carbohydrates (Schäfer *et al.*, 2003), or fast turnover of fine root (Norby *et al.*, 2004) and mycorrhizal biomass.

### 2. Soil carbon

In a review, Aerts (1997) showed that, on a global scale, climate (expressed as annual actual evapotranspiration) is the factor that best predicts first-year leaf litter-decay rates. A stimulation of leaf litter decomposition can therefore be anticipated as the

result of increasing temperature. Based on a study in four Canadian forests, litter decomposition was predicted to increase by 4–7% relative to the present rate, following an increase in temperature and precipitation estimated from a double [CO<sub>2</sub>] scenario (Moore *et al.*, 1999). The temperature response of litter at later stages of decomposition and of SOM is debatable, with some studies suggesting increasing sensitivity with decreasing quality (Ågren & Bosatta, 2002; Fierer *et al.*, 2005; Knorr *et al.*, 2005a) and others suggesting no effect (Giardina & Ryan, 2000; Fang *et al.*, 2005); see Davidson & Janssens (2006) for a recent review. Soil-warming experiments indicate that soil respiration, after an initial increase when the heating is first switched on, becomes comparable on unheated and heated plots (Luo *et al.*, 2001; Strömberg, 2001; Melillo *et al.*, 2002). It is possible that such transient initial increases in soil respiration occur, at least partly (Lin *et al.*, 2001), because of increased oxidation of the most labile soil C compounds in the heated plots, leading to the conclusion that, after some time, the decrease in litter quality in the heated plots compensates for the effect of the higher temperature (Kirschbaum, 2004; Eliasson *et al.*, 2005). It remains to be tested if acclimation of autotrophic (Atkin & Tjoelker, 2003) and microbial (Davidson & Janssens, 2006) respiration are also important factors.

## V. Fertilization and nitrogen deposition

### 1. Plant carbon

If trees respond to N deposition as in fertilization experiments, the leaf area of trees and stands is expected to increase with N deposition in N-limited forests (Linder & Murray, 1998; Ewers *et al.*, 2001; Sigurdsson *et al.*, 2002). In forest ecosystems with severe N limitation, N deposition is likely to increase foliar N concentration with a positive effect on photosynthetic rates and C sequestration, which is observed for oceanic spruce stands (Fig. 3a). Considering that production in most northern temperate and boreal forests is chronically restricted by lack of N (Tamm, 1991; Vitousek & Howarth, 1991), a clear relationship between N deposition and annual NEE ( $\approx$ CO<sub>2</sub> net flux,  $F_c$ ) could be expected (Fig. 3a). The lack of such a relationship shows that to account for effects of N deposition, all stand factors need to be included.

In ambient [CO<sub>2</sub>], increased allocation to both leaves and woody tissues was found in an N-fertilization study where the deposition rate was quadrupled in an area already thought to be N-saturated because of a heavy N-deposition load (Nilsson & Wiklund, 1995). From this and other fertilization studies in both ambient and elevated [CO<sub>2</sub>], it can be inferred that the likely response to increasing N deposition is increased production of leaves and wood, including coarse roots (Oren *et al.*, 2001; Iivonen *et al.*, 2006). In ecosystems approaching N saturation, the effect of N deposition may be less pronounced or even reversed. Fifteen years of high N additions (15 g m<sup>-2</sup> yr<sup>-1</sup>) added to the forest floor in the Harvard Forest

Long-Term Research led to N saturation, evidenced by high N-leaching rates and considerably increased tree mortality, although with species differences (Magill *et al.*, 2004).

Increasing leaf area in fertilization experiments can also result in changes in canopy characteristics: for example, a more pronounced gradient in foliar characteristics down the canopy (Palmroth *et al.*, 2002), probably accompanied by reduced photosynthetic rates in the lower canopy, has been observed (Oren *et al.*, 1986). However, forest canopies have considerable acclimation capability. A consequence of this is that the distribution of N adjusts in relation to the distribution of absorbed photosynthetic photon flux density, so as to make effective use of both light and N in photosynthesis (Kull, 2002) leading to transient increase in needle-litter production.

All N deposition does not reach the soil surface, but part of the wet and dry deposition and gaseous forms of N may be directly absorbed in the canopy. The fraction of N entering the ecosystem through canopy uptake is difficult to quantify, and estimates range from a few per cent to 24% (Harrison *et al.*, 2000). It is possible that canopy uptake of N upsets the nutrient balance of trees, with detrimental effects on growth (Schulze, 1989), although this process has not been studied extensively in recent years.

### 2. Soil carbon

Studies of N effects on decomposition are, in most cases, based on experiments in which large amounts of N have been added once or just a few times. In most cases, the decomposition of leaf and needle litter has also been followed over short periods, with a maximum of 5–8 yr. We are aware of very few experiments in which (1) the effects of long-term additions of small amounts of N have been followed; and (2) the decomposition of SOM has been studied (excluding recent leaf litter). Effects of N fertilization on litter decomposition rates are contradictory (Hobbie, 2005), with some studies showing no effects (Prescott, 1995; Hobbie & Vitousek, 2000); other studies showing increased decomposition rates (Hobbie, 2000; Vestgarden, 2001); and still others showing decreased decomposition rates (Prescott, 1995; Magill & Aber, 1998). A recent meta-analysis by Knorr *et al.* (2005b) indicates, however, that litter decomposition is stimulated at sites with low ambient N deposition (<5 kg ha<sup>-1</sup> yr<sup>-1</sup>) and for high-quality (low-lignin) litters, whereas decomposition rates are reduced at sites with moderate levels of N deposition (5–10 kg ha<sup>-1</sup> yr<sup>-1</sup>) or for low-quality (typically high-lignin) litters.

From a theoretical point of view, Ågren *et al.* (2001) identified three variables that can decrease rates of mass loss and thus lead to retention of more C in the soil: (1) decreased decomposer growth rate; (2) increased decomposer efficiency (production-to-assimilation ratio); and (3) more rapid formation of recalcitrant compounds. After applying their model to data from a fertilizer experiment on loss of litter mass, changes in C chemistry, and N concentration, they found that

increased decomposer efficiency and more rapid formation of recalcitrant compounds were the most important variables explaining the observed decrease in mass-loss rates of litter of various origins.

Results from a study of N and C cycling in a north–south gradient in Europe are in line with observations by Fog (1988) – a positive relationship between C : N ratio and CO<sub>2</sub> evolution rate in the litter and humus layers (Fig. 5), but no clear relationship between C : N and CO<sub>2</sub> evolution rate in the mineral soil (Persson *et al.*, 2000). However, along the European gradient, many variables other than C : N might affect the mineralization rate. Manipulation of N at the same site can reduce these confounding variables. In two Swedish forest fertilization experiments (Norrliden and Stråsan), N was added annually over 23 and 27 yr, respectively. Laboratory incubations showed a 30% reduction of the mineralization rate in the mor layer of plots that had received N additions of 60 kg ha<sup>-1</sup> yr<sup>-1</sup> compared with unfertilized plots (Persson *et al.*, 2000). Results from modelling of bomb-<sup>14</sup>C data from the Norrliden experiment are in line with the results from these laboratory incubations, showing that 100 yr of addition of 30 kg N ha<sup>-1</sup> yr<sup>-1</sup> could result in a doubling (1.3 kg C m<sup>-2</sup>) of the amount of C stored in the mor layer (Franklin *et al.*, 2003). About 60% of this increase was estimated to be the result of decreased decomposition rate and the rest a result of increased litter production. The explanation for the decreased decomposition rate was a fertilizer-induced increase in decomposer efficiency (production-to-assimilation ratio), a more rapid rate of decrease in litter quality, and a decrease in decomposer basic growth rate (Franklin *et al.*, 2003). Interestingly, the addition of NPK fertilizer resulted in a 200% increase (2.6 kg C m<sup>-2</sup>) of C stored in the mor layer (Franklin *et al.*, 2003). Thus from the above studies it appears that N deposition will lead to a decrease of the mineralization rate and an accumulation of C in the mor layer.

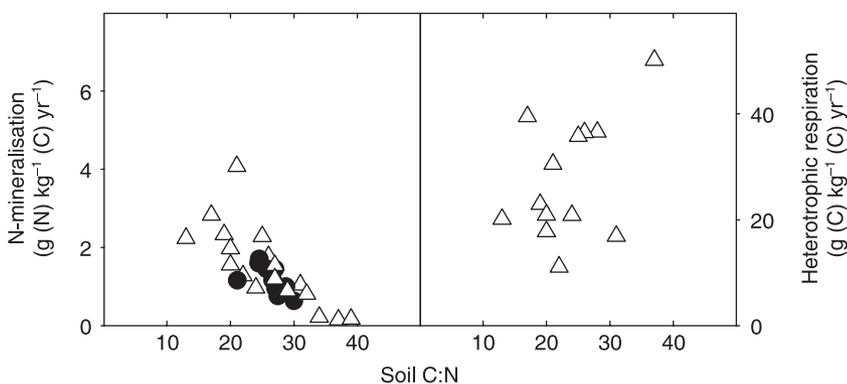
## VI. Disturbances and forest management

Disturbances such as fire, insect outbreaks, windthrow and harvesting have a very large effect on the C cycle in the short

term (years to decades), through reducing leaf area and by killing or removing trees that, in combination with the increased amount of dead material undergoing decomposition, may turn the disturbed area of forest into a temporary source of CO<sub>2</sub> (Kowalski *et al.*, 2003; Law *et al.*, 2003). Over the long term, the C lost in decomposition is replaced as the disturbed forest area regrows, so that net C storage over a disturbance cycle may approximate zero, as long as a forest replaces itself, or is replaced, and the disturbance frequencies do not change. Short-term increase in the frequency of fire may, however, cause progressive C losses. For example, annual C losses from fire in the Canadian boreal forest are estimated to be 10–30% of average NPP (Harden *et al.*, 2000), and current climate models predict a 25–50% increase in the area burned in the USA over the next 100 yr (Neilson & Drapek, 1998; Dale *et al.*, 2001). On the other hand, an increase in the interval between disturbances may allow the progressive accumulation of C to continue.

As the vegetation recovers after a disturbance and the canopy closes, a transition from C source to C sink occurs, the faster the transition, the more productive is the stand. Only 1 yr after coppicing, the GPP of the regrowing shoots of *Quercus cerris* counterbalances ecosystem respiration, whereas it takes 20 yr or more for a stand of slow-growing Scots pine (*P. sylvestris*) in a boreal environment to return to a net C sink after clear-cutting (Law *et al.*, 2001; Rannik *et al.*, 2002; Kowalski *et al.*, 2004). Similarly, on nutrient-poor sandy soils in the south-eastern USA, a *P. taeda* stand re-established LAI slowly and remained a source of C 6 yr after clear-cutting, whereas a fertilized stand returned to being a C sink within that time as LAI rapidly doubled (Lai *et al.*, 2002). Decomposition of organic matter resulting from harvest residues can dominate NEE during the recovery stage. Immediately after clear-cutting, when the new trees are small, R<sub>E</sub> is dominated by decomposition of the harvest residues, whereas heterotrophic respiration becomes more closely related to current production of trees as the stand ages (Janssens *et al.*, 2001; Falge *et al.*, 2002a, 2002b; Whitehead *et al.*, 2004).

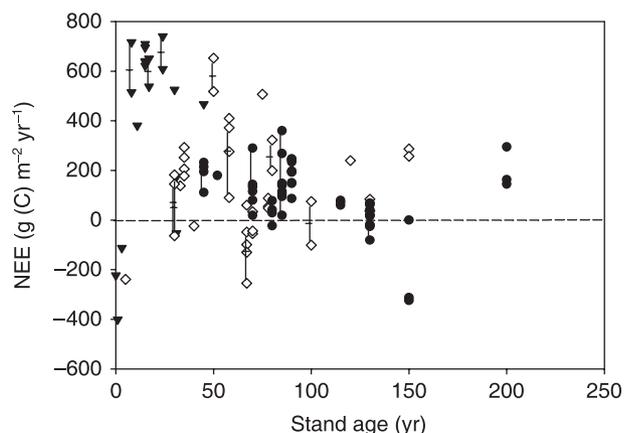
Management controls stand productivity by changing the competition and LAI of the canopy and thus modifying NEE.



**Fig. 5** Nitrogen mineralization and heterotrophic respiration in the humus layer as functions of soil C : N ratios. Swedish data (●) from Andersson (2002); European data (△) from Persson *et al.* (2000).

In general, stands with large LAI have higher NEE than stands with low LAI (Fig. 3b). Intensively managed forests behave as strong C sources following clear-cutting and site-preparation operations. They reach their maximal C-sink strength earlier than lightly managed or unmanaged forests. By comparison, the NEE-age curve is flattened and lengthened for lightly managed and unmanaged forests, both of which show a large scatter in annual NEE (Fig. 6). Apart from the Fyederovskoye spruce stand, situated at the northern tree line in the Russian taiga, which is a strong C source (Milyukova *et al.*, 2002), unmanaged stands are either close to neutral or weak C sinks in the postmaturation phase. In the long term, thinning has only very small effects on sequestration of C in commercial forests, as long as the thinning operations are not severe (Freeman *et al.*, 2005). The differences in C sequestration between managed and unmanaged forests will be most evident during the self-thinning phase in unmanaged forests. The recent history of the vegetation stand and soil appears to be of primary importance. For instance, the Swedish Norunda forest and the Belgium Brasschaat forest are thought to lose C from the soil stock and vegetation residues because of historical drainage and thinning, respectively (Lindroth *et al.*, 1998; Carrara *et al.*, 2003). There seems to be no consistent effect of management on mineral soil C stocks: both increases and decreases are observed, but N fertilization generally has a positive effect on soil C accumulation (Johnson & Curtis, 2001).

Any measures increasing the productivity of the forest ecosystem may increase C sequestration in the forest (Johnson *et al.*, 2002; Paul *et al.*, 2003). Therefore higher stocking throughout the rotation is preferable if management aims at a high C-sequestration capacity in the forest ecosystem. The productivity of forest ecosystems may be increased through



**Fig. 6** Annual net ecosystem exchange (NEE) according to the age of dominant trees for temperate and boreal forests as classified by management intensity.  $\nabla$ , plantations and coppiced stands;  $\diamond$ , lightly managed forest stands thinned or harvested by selection felling or clear-felling;  $\bullet$ , unmanaged forests. Values joined by a vertical line belong to a common site; horizontal dashed line, interannual mean value of the site (data in this figure are recalculated from the tables in Black *et al.*, 2005).

fertilization which, in the form of N combined with other nutrient elements, may drastically increase forest growth in the boreal and temperate regions (Tamm, 1991; Linder, 1995; Bergh *et al.*, 1999; Jarvis & Linder, 2000). At the same time, N fertilization may also decrease the decomposition of SOM in the long run, leading to an increasing stock of C in the soil profile (Johnson, 1992; de Wit & Kvindesland 1999; Johnson & Curtis, 2001; Nohrstedt, 2001; Freeman *et al.*, 2005).

The choice of tree species that are planted and the resulting stand composition may have a major impact on the C-sequestration capacity of the forest ecosystem. For example, mixing birch or other deciduous species with spruce and pine may enhance C sequestration (de Wit & Kvindesland 1999). On the other hand, forest ecosystems dominated by conifers may, in many cases, sequester C even more effectively and store C longer than ecosystems dominated by deciduous trees (Table 2). This is because the growth rate of many coniferous species is higher over longer periods than that of many deciduous species (cf. Cannell, 1989). Furthermore, the decomposition rate of coniferous litter is generally lower than that of deciduous litter.

In certain regions, forest management induces the conversion of complex forests to more simple stands, often dominated by one or a few species with similar characteristics. For example, the warm temperate forests of the south-eastern USA, the region of highest forest production activity in the USA, are undergoing a rapid conversion to evergreen pine plantations, partly from natural pine and partly from oak–pine forest, but also from pure hardwood stands (Birdsey *et al.*, 2006). Palmroth *et al.* (2005) assessed the effects on seasonal and annual forest floor  $\text{CO}_2$  efflux and total belowground C allocation, focusing on a mature oak–hickory forest and a maturing loblolly pine plantation closely located on similar soils. The estimates of total belowground C allocation were inferred from the measured  $\text{CO}_2$  efflux, litter fall, and published estimates of changes in C storage in the litter layer and mineral soil (Giardina & Ryan, 2002; Lichter *et al.*, 2005). Excluding winter months,  $\text{CO}_2$  efflux was higher in the oak–hickory stand compared with the adjacent loblolly pine plantation. The higher  $\text{CO}_2$  efflux in oak–hickory resulted primarily from higher soil temperature, augmented by lower sensitivity to soil moisture. On an annual basis, the combined effect was a similar annual  $\text{CO}_2$  efflux at the two sites during a wet year, but higher annual  $\text{CO}_2$  efflux in the oak–hickory than in the loblolly pine stand during a severe drought year. In the wetter year, total belowground C allocation indicated that C in the litter–soil system was at steady state in the oak–hickory stand, and was accruing in the loblolly pine plantation. The oak–hickory stand was, however, probably losing C from the mineral soil during the severe drought year of 2002, while the loblolly pine was accumulating C at a lower rate, as a result of loss of C from the litter layer. Nevertheless, the results indicate that C accumulation in litter and soil of pine plantations in this region is likely to be higher than in mature

**Table 2** Qualitative effects on average carbon stocks of management operation in managed forests over a rotation period compared with the rotation period prior to management (modified from Freeman *et al.*, 2005)

Management measure	Soil C stock	Biomass C stock	Ecosystem C stock
Stand initiation phase			
Prescribed burning*	Decreasing	Decreasing, neutral or increasing	Decreasing, neutral or increasing
Drainage of peatland†	Decreasing	Increasing	Decreasing, neutral or increasing
Site preparation method‡			
Low-intensive	Neutral	Increasing	Increasing
Intensive	Decreasing	Increasing	Decreasing, neutral or increasing
Tree species change§			
To conifers from broadleaves	Increasing	Increasing	Increasing
To broadleaves from conifers	Decreasing	Decreasing	Decreasing
To mixed conifers and broadleaves from mono-specific coniferous	Neutral or decreasing	Neutral or decreasing	Neutral or decreasing
Stem exclusion phase			
Thinning method¶	Neutral or decreasing	Decreasing	Decreasing
Fertilization**	Increasing	Increasing	Increasing
Increased rotation length††	Decreasing, neutral or increasing	Increasing	Increasing
Harvesting method‡‡	Decreasing, neutral or increasing	Decreasing, neutral or increasing	Decreasing, neutral or increasing

\*Biomass and ecosystem C stocks depend on regeneration success and nutrient loss.

†Ecosystem C stock depends on loss from soil and gain in biomass.

‡Ecosystem C stock after intensive preparation depends on loss from soil and gain in biomass.

§Soil C depends on the decomposition rate which is generally lower for conifer litter than for broadleaf litter. Biomass and ecosystem C depend on the growth rate which is higher over longer periods for many conifer species than for broadleaf species.

¶Removal of thinning residues can give large transient reductions in soil C.

\*\*Higher production increases all C stocks. N fertilization increases litter production and may reduce decomposition in soil in the long term.

††All C stocks depend on developmental stage of the forest when the rotation period is prolonged and on the thinning method.

‡‡Soil C depends on the removal of residues. Biomass and ecosystem C for the following rotation period depend on how regeneration and growth conditions are affected by the harvesting operation.

hardwood forests. It is essential, however, to consider the fate of the soil C already stored in mature forests when these undergo large-scale conversion to managed plantations.

In a broader sense, when considering the effects of forest management one should also consider the life cycle of the forest products removed (Harmon *et al.*, 1990; Ericsson *et al.*, in press). If all the wood harvested is used for products with a long lifespan (for example, constructional timber in buildings instead of concrete), much more C will be gained. Also, when the forest products are used for short-lifespan products, such as biofuel, instead of using fossil fuels, there will be an important net gain of C (Ericsson *et al.*, in press), although C storage in soil, biomass and forest products is lower.

## VII. Feedbacks and interactions

The simple responses depicted above are complicated by factors that affect several fluxes at the same time, and by changes in one part of the system that feed back to other parts

of the system. For example, the direct response of photosynthesis,  $P$ , to an increase in  $[\text{CO}_2]$  will eventually require additional N, and the NPP response will therefore decline as N limitation sets in (Rastetter *et al.*, 1997). The most severe feedback effects are likely to appear at the ecosystem scale, but there are also feedback effects at the plant and soil scales. At the plant scale, the reason for the conservative NPP : GPP ratio of approx. 0.5 (Waring *et al.*, 1998) may be a carbohydrate-availability feedback acting on respiration (Dewar *et al.*, 1999). At the soil scale, an increase in decomposition rate is likely to increase the amount of available inorganic N, but there have been observations that an increased amount of inorganic N can slow down decomposition (Fog, 1988; Ågren *et al.*, 2001).

The extra C acquired by northern forests as a result of the increasing length of the growing season (the main temperature response), higher LAI (the main N-deposition response), and higher photosynthetic rate (the main  $[\text{CO}_2]$  response) is partitioned to respiration and production of different plant parts. This partitioning is likely to be affected by the amount

of additional carbohydrates available relative to other resources. Increasing production requires the use of additional C in growth respiration, and a larger standing biomass may utilize additional C as well (but c.f. Ryan & Waring, 1992; Ryan *et al.*, 1994).

Elevated [CO<sub>2</sub>] may result in the production of biomass with lower N concentration (Cotrufo *et al.*, 1998b), and this may offset the increase in respiration resulting from the larger standing biomass; respiration being proportional to the amount of N (Ryan, 1991). Where nutrients limit growth, production of leaf and woody biomass may not increase in elevated [CO<sub>2</sub>] (Oren *et al.*, 2001; Sigurdsson *et al.*, 2001; Körner *et al.*, 2005). Most fertilization studies on N-limited sites show that increasing nutrient availability does not increase fine-root biomass, and may decrease the number of mycorrhizal root tips (Meyer *et al.*, 1988; Fransson *et al.*, 2000; Parrent *et al.*, 2006) as well as the production of mycorrhizal mycelium in the soil (Nilsson & Wallander, 2003). An N-deposition study suggested that fine-root biomass can decrease as a result of enhanced deposition, but that root turnover and thus production may increase (Gundersen *et al.*, 1998; Nadelhoffer, 2000).

Increasing air temperatures with climate change are expected to result in higher soil temperature. A soil-warming experiment in a boreal Norway spruce forest resulted in increased N availability, leading to substantial increases in tree growth (Strömberg & Linder, 2002), and to likely increases in ecosystem C storage because the C : N of vegetation is much larger than the C : N of the SOM that has been decomposed to release N. It is not known, however, how sustainable such increases are. With an increase in N availability, an increase in leaf area, and a consequent increase in tree growth, one might justifiably expect a positive feedback resulting from enhanced future litter deposition, on a time scale of several years in the case of evergreens.

We also emphasize that all FACE studies induce a step change in atmospheric [CO<sub>2</sub>]. Step changes may induce a sudden, significant increase of labile C in the soil, stimulating rhizosphere activity with consequent priming of the decomposition of old stable organic matter (Hoosbeek *et al.*, 2004). It is likely that, with a gradual annual increment of atmospheric [CO<sub>2</sub>], the pre-existing forest soil C will not experience a sudden increase of C input, and thus priming of old SOM may be less important than the factors promoting a progressive increase in SOC stock.

Links between litter quality and soil C decomposition under changes in soil temperature are not always straightforward. Plant metabolism (Högberg *et al.*, 2001; Olsson *et al.*, 2005) and the decomposition of recently produced organic material (Trumbore, 2000; Giardina & Ryan, 2002; Giardina *et al.*, 2004) generate most of the 'soil' respiration, which strongly reflects plant metabolism (Ekblad & Högberg, 2001; Bowling *et al.*, 2002; Ekblad *et al.*, 2005; Högberg & Read, 2006), thus it is not always easy to determine if increased soil

respiration originates from autotrophic or heterotrophic activity. The SOC content had increased significantly in a sweetgum (*L. styraciflua*) plantation after 5 yr of FACE under nonlimiting N conditions (Jastrow *et al.*, 2005). On the other hand, Hoosbeek *et al.* (2004) reported a decreased C stock in soils exposed to elevated [CO<sub>2</sub>] at the end of a 3-yr rotation of a poplar plantation. This change occurred despite larger litter inputs, and was attributed to priming of decomposition of native SOC. Also, soils receiving lower-quality litter may in fact have higher specific decomposition rates (Giardina *et al.*, 2001).

In a transient system, single-factor responses from short-term experiments can be misleading for long-term predictions, because slowly evolving feedback as well as acclimation processes do not have time to exert their full impacts (Hanson *et al.*, 2005). This is particularly relevant when results from experimental studies, which are usually short term, are compared with results from observational studies, in which feedback processes at all temporal scales operate. Moreover, the long-term responses tend to be dominated by feedback loops. The recalcitrant soil C, the largest terrestrial C pool, contributes only a minor portion to soil CO<sub>2</sub> efflux at any moment in time (Trumbore, 2000; Giardina *et al.*, 2004). Thus soil respiration is a good indicator of metabolism, but a poor indicator of changes in long-term soil C storage.

## VIII. Will we have forest carbon sinks in the future?

It is not in doubt that newly established young forests will continue to be C sinks for the foreseeable future. The key question is whether the mature forests that are C sinks today will continue to be sinks as the climate changes. The C balance is particularly vulnerable because the balance is the small difference between a large input and a large output of C. If the input diminishes, or the output increases, as a result of global climate change, a C sink may diminish to zero and the forest may become a C source. Forest ecosystem models (e.g. Churkina *et al.*, 2003) indicate that the additional terrestrial sink arising from global climate change is likely to be maintained in the short term (over several decades), but may gradually diminish in the medium term. One reason for this is that the capacity of some forests to sequester C may be approached; another is that photosynthesis will increase less as the [CO<sub>2</sub>] concentration continues to rise, whereas respiration is expected to continue to increase with the rise in temperature. The balance between forest photosynthesis and respiration is crucially dependent on the nutrient dynamics of the forest ecosystem, as well as on other environmental variables. Simplistic models forecasting that stand photosynthesis will be overtaken by stand respiration, purely on the basis of short-term responses of photosynthesis to [CO<sub>2</sub>] and respiration to temperature, should be treated with great caution. Because of current limitations on our understanding with respect to acclimation of the physiological processes, the climatic constraints, and

feedbacks among these processes – particularly those acting at the biome scale – projections of C-sink strengths beyond a few decades are highly uncertain.

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