

## LETTERS

# The human footprint in the carbon cycle of temperate and boreal forests

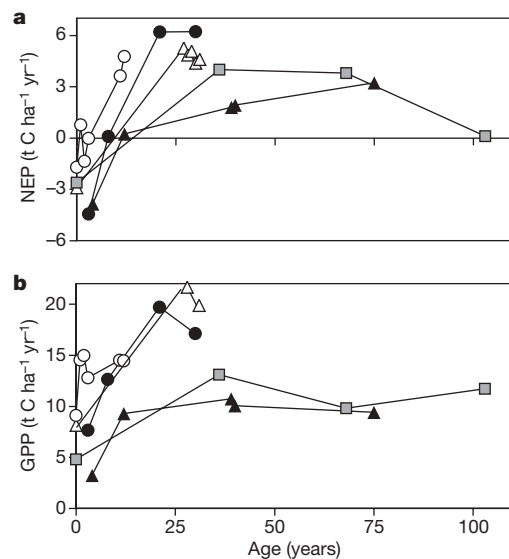
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Temperate and boreal forests in the Northern Hemisphere cover an area of about  $2 \times 10^7$  square kilometres and act as a substantial carbon sink (0.6–0.7 petagrams of carbon per year)<sup>1</sup>. Although forest expansion following agricultural abandonment is certainly responsible for an important fraction of this carbon sink activity, the additional effects on the carbon balance of established forests of increased atmospheric carbon dioxide, increasing temperatures, changes in management practices and nitrogen deposition are difficult to disentangle, despite an extensive network of measurement stations<sup>2,3</sup>. The relevance of this measurement effort has also been questioned<sup>4</sup>, because spot measurements fail to take into account the role of disturbances, either natural (fire, pests, windstorms) or anthropogenic (forest harvesting). Here we show that the temporal dynamics following stand-replacing disturbances do indeed account for a very large fraction of the overall variability in forest carbon sequestration. After the confounding effects of disturbance have been factored out, however, forest net carbon sequestration is found to be overwhelmingly driven by nitrogen deposition, largely the result of anthropogenic activities<sup>5</sup>. The effect is always positive over the range of nitrogen deposition covered by currently available data sets, casting doubts on the risk of widespread ecosystem nitrogen saturation<sup>6</sup> under natural conditions. The results demonstrate that mankind is ultimately controlling the carbon balance of temperate and boreal forests, either directly (through forest management) or indirectly (through nitrogen deposition).

The life of forest ecosystems is punctuated by stand-replacing disturbances, mainly associated with fire or forest management. After each event, the forest is typically a net source of carbon (C) over the first years, followed by a broad peak in C sequestration (NEP, net ecosystem production; Fig. 1a) and gross primary production (GPP; Fig. 1b) in maturing forests. In older stands, NEP usually declines as a result of the age-related reduction in growth<sup>7</sup>. Age effects account for 92% of the total variability in NEP in five chronosequences analysed as part of the CARBOEUROPE project (<http://www.bgc-jena.mpg.de/public/carboeur/>), spanning from boreal coniferous to temperate broadleaf forests. Forested landscapes, however, are a patchwork of stands of different age, and the mean C sequestration at this scale is more closely approximated by the average NEP over the entire rotation, that is, between two subsequent stand-replacing events (NEP<sub>av</sub>). When combining data from the five CARBOEUROPE chronosequences with several published literature data sets from boreal and

temperate established forests (Table 1), NEP<sub>av</sub> amounts to only 56% of peak NEP ( $38 \pm 15\%$  s.d. for individual forests; Fig. 2). Such a correction for disturbance effects could help reconcile flux- and inventory-based estimates of net C sequestration by terrestrial vegetation<sup>4</sup>.

Because of their magnitude, age-related dynamics make it difficult to assess what other factors control forest C sequestration at the regional and global level<sup>8</sup>. We therefore filtered out the effects of age by taking the average of C fluxes over the entire rotation. Both ecosystem respiration (RE<sub>av</sub>) and gross primary production (GPP<sub>av</sub>) were positively correlated with mean annual temperature at the site ( $R^2 = 0.83$  and  $0.82$ , respectively); only one forest in the entire data set was known to be severely affected by water stress<sup>9</sup>, which appeared to reduce in parallel both photosynthesis and respiration. The correlation with temperature improved significantly when this dry site was excluded from the analysis (Fig. 3a and b), so highlighting the primary role of heat and



**Figure 1 | Age-related dynamics of C balance components in forest ecosystems following disturbance.** **a**, Dynamics of NEP; **b**, dynamics of GPP in five CARBOEUROPE chronosequences across Europe. Symbols refer to the following site codes (see Table 1): 7, black circles; 10, white triangles; 12, grey squares; 13, black triangles; 19, white circles.

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**Table 1 | Main site characteristics and C flux components of forest chronosequences used in the analysis**

Main species	Site code	Age (years)	Latitude (°N)	Longitude (°E)	Data type	Disturbance type	GPP <sub>av</sub> (t C ha <sup>-1</sup> yr <sup>-1</sup> )	RE <sub>av</sub> (t C ha <sup>-1</sup> yr <sup>-1</sup> )	NEP <sub>av</sub> (t C ha <sup>-1</sup> yr <sup>-1</sup> )	Maximum NEP (t C ha <sup>-1</sup> yr <sup>-1</sup> )	Reference
<i>Fagus sylvatica</i>	1	0–250*	51° 05'	10° 27'	EC	AB	15.6	10.7	4.9		23
	2	30–153	51° 20'	10° 22'	B	SW	16.1	11.5	4.6		24
<i>Nothofagus solandrii</i>	3	10–>160	43° 15'	171° 35'	B	WT			0.3		22
<i>Picea mariana</i>	4	3–151	55° 53'	–98° 20'	B	FF	6.6	6.2	0.4	1.1	25
	5	3–151	55° 53'	–98° 20'	B	FF	7.1	6.4	0.7	2.9	25
	6	11–130	55° 54'	–98° 28'	EC	FF	6.7	6.5	0.2	1.2	26
<i>Picea sitchensis</i>	7	3–30	55° 10'	2° 03'	EC, B	CC	15.4	12.7	2.7	5.5	†
<i>Pinus banksiana</i>	8	1–72	44° 35'	–84° 15'	B	FF			0.4	1.8	27
	9	0–79	53° 54'	–104° 39'	B	CC, FF	5.5	5.4	0.1	0.5	28
<i>Pinus pinaster</i>	10	0–50	44° 35'	0° 52'	EC, B	CC	18.3	14.8	3.6	6.5	†
<i>Pinus ponderosa</i>	11	9–316	44° 24'	–121° 36'	B	CC	7.8	7.2	0.6	1.6	9
<i>Pinus sylvestris</i>	12	0–103	60° 05'	17° 28'	EC, B	CC	10.1	8.5	1.6	3.7	†
	13	4–75	61° 51'	24° 17'	EC, B	CC	9.5	8.4	1.1	2.3	†
	14	12–266	60° 43'	89° 08'	B	FF	7.4	7.0	0.4	0.6	21
	15	14–215	60° 43'	89° 08'	B	FF	4.0	3.9	0.1	0.2	21
	16	2–383	60° 43'	89° 08'	B	FF	5.5	5.4	0.1	0.4	21
	17	2–95	60° 43'	89° 08'	B	FF	4.1	3.6	0.5	1.3	21
<i>Pseudotsuga menziesii</i>	18	0–500*	45° 49'	–121° 57'	B	AB	12.7	12.5	0.2		29
<i>Quercus cerris</i>	19	1–17	42° 24'	11° 55'	EC, B	CO	16.1	13.7	2.4	4.4	†
<i>Tsuga martensiana</i>	20	14–262	43° 30'	–122° 00'	B	PE			0.1	0.6	30

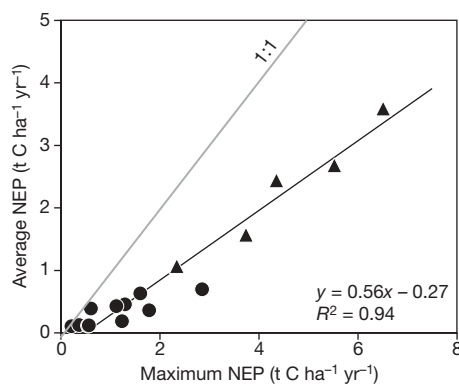
EC, eddy covariance; B, biomass; CC, clear-cut; CO, coppice; SW, shelterwood; AB, abandoned; FF, forest fire; PE, pests; WT, windthrow. \*Uneven aged. †This study.

water stress in controlling the individual components of forest C balance. This confirms previous studies at the continental scale<sup>2,3</sup>, although with much lower scatter owing to the removal of age effects. In contrast with GPP<sub>av</sub> and RE<sub>av</sub>, mean NEP (NEP<sub>av</sub> = GPP<sub>av</sub> – RE<sub>av</sub>) is only weakly correlated with temperature (Fig. 3c). No correlation was found with either annual precipitation ( $R^2 = 0.01$ ) or site latitude ( $R^2 = 0.04$ ), leaving open the question of what could be driving C sequestration in boreal and temperate forests.

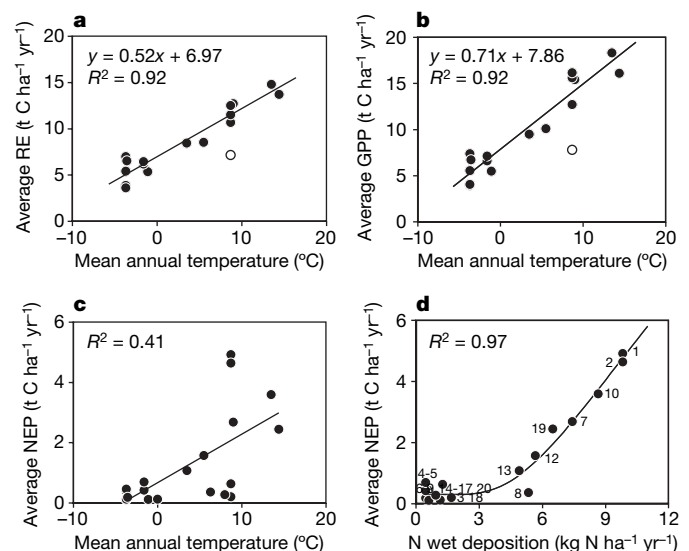
It was first recognized in the 1980s that human activities, by releasing into the atmosphere unprecedented amounts of active nitrogen (N), were not just altering the global N cycle<sup>5</sup>, but also resulting in the eutrophication of large parts of the biosphere<sup>10</sup>. Boreal and temperate forest ecosystems are generally N-limited and the addition of N through wet and dry deposition has been hypothesized to result in the stimulation of forest growth and C sequestration<sup>6</sup>. Earlier model simulations suggested that N deposition could account for an increased C sequestration of 0.44–0.74 Pg yr<sup>-1</sup>, mainly in temperate and boreal regions<sup>11</sup>. More recently, the relevance of N deposition for forest C sequestration has been questioned, on the basis of manipulation studies<sup>12</sup> and modelling extrapolation from N budgets<sup>13</sup>. In both studies, however, C sequestration was estimated from N fluxes themselves, assuming fixed C:N ratios. The relationship between N deposition and forest C sequestration has never been tested through direct observations across a range of forest conditions.

Using recently released gridded maps of N fluxes across Western Europe and North America<sup>14</sup>, we found a tight relationship between

average C sequestration and wet N deposition in the corresponding cell (Fig. 3d;  $R^2 = 0.97$ ), which is largely obscured by age effects when data from individual stands are considered. We used wet rather than total N deposition because dry deposition was not measured directly, but derived from transfer models based on a limited data set of atmospheric concentrations, resulting in very large uncertainties<sup>5</sup>. The substantial net C sequestration by many temperate forests appears to be overwhelmingly determined by the additional input of N induced by human activities. We therefore hypothesize that the observed response of GPP<sub>av</sub> and RE<sub>av</sub> to temperature is mainly controlled by soil organic matter decomposition, which releases the nutrients needed for photosynthesis and growth, and that human activities, by adding an additional source of N readily available to plants, have determined an imbalance between the two components of the feed-back loop, so resulting in the net sequestration of C by forest ecosystems. Although a comprehensive analysis should consider in detail the distribution of existing forests and their uneven age structure, as well as the loss of C



**Figure 2 | Relationship between average NEP over the entire rotation and peak NEP in mature stands.** Data from five CARBOEUROPE chronosequences (triangles) have been combined with eleven other literature data sets (see Table 1). Estimates of average and peak NEP are based on interpolated values of C fluxes; a linear function has been fitted by Type II regression ( $n = 16$ ).



**Figure 3 | Environmental control of average C exchange over an entire rotation.** Linear relationships between average RE (a) and average ecosystem GPP (b) and mean annual temperature at the study sites. In both a and b, the only drought-prone site<sup>9</sup> (white circle) has been excluded from the analysis. c, Average NEP is only poorly correlated to temperature. d, Average NEP is strongly related to N deposition. Numbers refer to site codes in Table 1. An Arrhenius function has been empirically fitted onto the entire data set ( $n = 20$ ).

through wildfire and logging, this could amount to an important fraction of the estimated C sink in the Northern Hemisphere<sup>1</sup>.

The proposed mechanism of ecosystem response to N deposition implies that plants can readily access this additional nutrient source, in contrast with the results of several manipulative studies<sup>12</sup>. Under conditions of long-term, low-dose fertilization, however, plants are effective competitors for available N (ref. 15); moreover, their ability to compete for N would appear to increase with N availability, as the microbial demand for N becomes saturated by local organic sources with progressively lower C:N (ref. 15, 16). This could explain the increasing slope of the NEP<sub>av</sub> response at high levels of N deposition (Fig. 3d), as more and more nutrients would be absorbed by plants and used for the production of woody biomass, with a high C:N ratio.

Are temperate and boreal forest ecosystems bound to become themselves saturated with N, resulting in forest dieback and a reduction in C sequestration<sup>9</sup>? Long-term studies of N enrichment in forests have demonstrated that ecosystem function responds to addition rate, rather than cumulated N input, and that although intermediate deposition levels could have beneficial effects, these could disappear at super-optimal N levels<sup>17</sup>. No signs of N saturation were apparent in our data set (Fig. 3d), which explored a broad range of wet deposition up to 9.8 kg N ha<sup>-1</sup> yr<sup>-1</sup> (~15 kg N ha<sup>-1</sup> yr<sup>-1</sup> of total N deposition), representative of more than 90% of the overall surface of Western Europe and the conterminous United States<sup>14</sup>. Long-term manipulation studies indicate that only at N addition levels of 50–60 kg N ha<sup>-1</sup> yr<sup>-1</sup> do clear signs of soil acidification, nutrient imbalances and tree damage become apparent<sup>17,18</sup>. Although these values are in excess of current maximum levels of atmospheric N deposition<sup>14</sup>, even higher rates are occasionally recorded and could occur in the future over entire regions<sup>5</sup>. Further chronosequence studies in selected areas with high N deposition could help us understand if the beneficial effects of N fertilization on the terrestrial C sink can be expected to persist over the next century.

## METHODS SUMMARY

Both C stocks and C fluxes<sup>2</sup> were measured in five representative forest chronosequences throughout Europe (Table 1), which comprised newly harvested, young and mature stands in the same locality. At each site, GPP and RE were also computed from NEP data. Data from 13 additional chronosequences and two uneven-aged stands were drawn from the literature (Table 1). When estimates based on the eddy-covariance technique were not available, GPP was derived from annual net primary production (NPP), assuming a constant relationship<sup>19</sup>, and RE estimated as the difference from NEP. All chronosequences were located either in natural forests or in plantations at least at second rotation and were not actively fertilized.

The chronosequence approach quantifies ecosystem C sink capacity at several stages in forest development; modelling tools were used to interpolate the resulting information over the entire rotation. A process-based approach was applied in the case of CARBOEUROPE chronosequences, for which direct flux and stock data were available, by linking two well-documented and tested ecosystem models<sup>19,20</sup>. In the case of literature chronosequences, flux integrals over the entire rotation were obtained by fitting suitable empirical equations<sup>9,21</sup> onto flux or ecosystem C data. In just one case<sup>22</sup>, because of the limited sample size, NEP<sub>av</sub> was estimated from the difference in ecosystem C between the newly regenerated stand and the old stand.

Estimates of N wet deposition in 1990 for sites in Western Europe and the conterminous United States were derived from recently published gridded maps<sup>14</sup>. Additional data for 1993 for the rest of the globe were derived from model simulations<sup>5</sup>; estimates of wet N deposition were then derived from modelled values of total N deposition, based on a correlation of values in the previous data set.

**Full Methods** and any associated references are available in the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

Received 13 November 2006; accepted 11 April 2007.

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

**Acknowledgements** This work was supported by the European Commission (General Directorate XII, CARBO-AGE project in the CARBOEUROPE cluster) and further supported by several national programmes. F.M. was also supported by the MIUR Carboltaly Project and by Società Produttori Sementi (Fondazione Cassa di Risparmio in Bologna) through the 'Selvicoltura' project.

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## METHODS

The analysis was based on a combination of measurements from five European chronosequences, collected as part of the CARBOEUROPE project, and literature data from a total of 15 chronosequences or uneven aged stands. A chronosequence is defined as a collection of forest stands of different age but otherwise homogeneous for plant material and environmental conditions; the footprint area of a chronosequence is larger than those generally studied in manipulation experiments, partly compensating for the lack of experimental replicates. All chronosequences were located either in natural forests or in plantations at least at second rotation and were not actively fertilized.

**Description of CARBOEUROPE chronosequences.** We identified five representative managed forests throughout Europe (see Table 1), which comprised newly harvested, young and mature stands in the same locality. The UK series consists of stands of *Picea sitchensis* at Harwood in northwest England; soils are predominantly peaty gleys, formed over glacial tills. The forest is managed by clear-cutting; the usual rotation is 40 years, and the data reported here are from the second rotation. Measurements were taken in stands 0, 7, 21 and 30 years old. The Italian site is a coppice with standards of *Quercus cerris* at Roccarespanpani in Central Italy. The soil is a Luvisol on a volcanic bedrock. The rotation length is 15–20 years. The ages of the available stands span the entire rotation: data are available for ages 1, 4, 10 and 17 years. The Finnish series consists of stands of *Pinus sylvestris* at Juupajoki in Southern Finland, on sandy glacial till of moderate fertility; the 40-year-old stand is 5 km away, in Hyytiälä, on coarse sandy glacial till. The rotation length is typically 80 years; the stands analysed are 3, 10, 40 and 75 years old. The Swedish sites are in Central Sweden, at Skyttorp (0, 30 and 60 years) and at Norunda (100 years); all the stands are dominated by *P. sylvestris*. The typical rotation length is about 100 years. The soil is a deep, boulder-rich sandy glacial till. The French site is part of Les Landes forest in southwestern France, and consists of mono-specific *Pinus pinaster* stands 0, 16, 26 and 50 years old on spodic sands. The typical rotation length is 50 years at the site.

Both C stocks (in soils, litter, woody debris and vegetation) and C fluxes were measured at each stand in the chronosequence; each stand in a chronosequence was large enough to satisfy conditions for measurement of CO<sub>2</sub> fluxes by the eddy covariance technique<sup>31</sup>. At each site, GPP and RE were also computed from NEP data, by assuming that respiration by day is the same as that at night after adjustment for the effect of the diurnal temperature cycle.

**Literature data sets.** Data from 13 additional chronosequences and 2 uneven-aged stands from boreal and temperate forests were drawn from the literature (see Table 1). The data set comprised only one chronosequence from the Southern Hemisphere. Direct measurements of NEP or ecosystem C were used for the estimation of average NEP over the entire rotation. C flux estimates in literature chronosequences were based either on the eddy-covariance technique or on biometric measurements (as detailed in Supplementary Table 1, see Supplementary Information). When data were provided only in graphical format, the relevant figure was captured from the electronic paper using commercial software (Paint Shop Pro 4.12, JASC) and individual datapoints digitized using the Un-Scan-It 5.0 dedicated software (Silk Scientific). When estimates based on the eddy-covariance technique were not available, GPP was derived from estimates of annual NPP, assuming a constant ratio<sup>32</sup>, and RE was estimated as the difference from NEP.

**Computation of average C fluxes in CARBOEUROPE chronosequences.** Although the chronosequence approach quantifies ecosystem C sink capacity at several stages in forest development, modelling tools are needed to interpolate the resulting information over the entire rotation. While such an integration procedure is needed to correct for any biases resulting from the limited sample size of each chronosequence, very similar results are obtained when raw means (and maxima) of field measurements are used instead (see Supplementary Information). A process-based approach was applied in the case of CARBOEUROPE chronosequences, for which direct flux and stock data were available, by linking two well-documented and tested ecosystem models. The 3PG-3 model stems from the combination of the 3PG (use of Physiological Principles in Predicting Growth) model<sup>19</sup>, to represent the NPP and growth of a forest stand, and the ICBM (Introductory Carbon Balance Model) model<sup>20</sup> for belowground C dynamics. The two models have been extensively documented and tested<sup>19,20,33–37</sup>. In addition, a third component has been added to represent the C exchange by the forest understorey (hence the suffix in 3PG-3), with a structure derived from the 3PG model with further simplifications.

**General model structure.** Because the aim of the model is to capture age-related differences among stands in a chronosequence, all experiencing the same conditions, the model overlooks the detailed response of primary production to individual environment factors, capturing it as a single reduction coefficient for the whole chronosequence irrespective of stand age. A single reduction

factor also captures the response of soil heterotrophic respiration to the soil environment (temperature, humidity, soil texture), irrespective of stand age. Age is assumed to have a direct effect (that is independent from the dynamics of C stocks) only on light-use efficiency, as described below. Because the seasonal dynamics of environmental factors are neglected, an annual time step is adopted throughout.

**NEP.** The representation of forest NPP is based on the light-use efficiency approach<sup>38</sup>. The amount of photosynthetically active radiation absorbed by the stand over the year  $\Phi_{pa}$  is a function of incoming radiation  $\Phi_p$  and stand foliage C ( $C_f$ ), following Beer's law:

$$\Phi_{pa} = \Phi_p(1-a)[1 - \exp(-k \times SLA \times C_f)] \quad (1)$$

where  $a$  is canopy albedo,  $k$  is a light extinction coefficient (of value 0.5 for spherically distributed leaves) and SLA is foliage-specific leaf area (expressed in terms of leaf C content). Stand GPP is assumed to be linearly proportional to absorbed light:

$$GPP = \varepsilon \Phi_{pa} \quad (2)$$

Radiation light-use efficiency  $\varepsilon$  is reduced below its potential value  $\varepsilon_0$  as a result of environmental and age-related effects:

$$\varepsilon = \varepsilon_0 f_{age} f_{tot} \quad (3)$$

The empirical parameter  $f_{tot}$  captures the combined effects of all environmental factors over the entire season and is assumed to be independent of stand age. The direct effects of age  $A$  are captured by the parameter  $f_{age}$ , defined as<sup>19</sup>:

$$f_{age} = \frac{1}{1 + (A/A_{0.5})^4} \quad (4)$$

where the parameter  $A_{0.5}$  is the age corresponding to a 50% reduction in light-use efficiency. Stand NPP is finally assumed to be a constant fraction of GPP<sup>32</sup>. The same approach is applied to understorey primary production. The amount of light reaching the understorey  $\Phi_p^{und}$ , however, is first reduced by overstorey interception. Moreover, the light-use efficiency of the understorey is not reduced by age but only by the environment through the reduction factor  $f_{tot}^{und}$ .

**Growth and litter production.** Available C is assumed to be allocated between foliage ( $C_f$ ), fine root ( $C_r$ ) and woody biomass ( $C_w$ ; including coarse roots and stumps) in proportion to allocation coefficients  $\eta_f$ ,  $\eta_r$  and  $\eta_w$ , respectively. A constant value is assumed for allocation to foliage<sup>39</sup>. Allocation to roots, on the contrary, is assumed to increase in response to both environmental stress and age, in parallel with the reduction in light-use efficiency:

$$\eta_r = \frac{0.8}{1 + 2.5m \times f_{tot} f_{age}} \quad (5)$$

The empirical parameter  $m$  captures the effects of soil fertility on fine root growth, and increases with soil fertility. Allocation to wood production is represented as residual growth. Annual changes in the  $i$ -th tree compartment (foliage, fine root and woody tissues) are represented as the difference between new growth and litter losses:

$$\frac{\Delta C_i}{\Delta t} = NPP \eta_i - C_i \gamma_i \quad (6)$$

where the parameter  $\gamma_i$  represents the annual mortality of the  $i$ -th compartment and is equal to zero in the case of woody biomass. Steady-state conditions are assumed for the understorey; understorey litter production is therefore assumed to be equal to the corresponding NPP<sub>und</sub>.

**Soil respiration and net ecosystem exchange.** The representation of soil organic matter (SOM) dynamics is based on the two-compartment ICBM model<sup>20</sup>. A young (that is, readily decomposable) and an old (that is, refractory) SOM compartment, with widely different residence times, are distinguished in the model.

The annual change in the biomass  $Y$  of the young SOM compartment is the difference of litter input (from trees and the understorey) and young SOM decomposition, which is assumed to be proportional to  $Y$ :

$$\frac{\Delta Y}{\Delta t} = (C_f \gamma_f + C_r \gamma_r + NPP_{und}) - r k_1 Y \quad (7)$$

The empirical parameter  $r$  captures the combined effects of temperature, humidity and soil texture on the decomposition parameter  $k_1$ , which represents unit  $Y$  decomposition under standard conditions. Young SOM decomposition is partly lost as respiration, the remaining being transferred to the old SOM compartment

through humification. Young SOM respiration is expressed as:

$$R_{\text{SOM}}^{\text{Y}} = (1-h)r k_1 Y \quad (8)$$

where  $h$  is a humification coefficient. The annual change in old SOM biomass  $O$  is therefore equal to:

$$\frac{\Delta O}{\Delta t} = r(k_1 Y h - k_2 O) \quad (9)$$

where  $k_2$  represents unit  $O$  decomposition under standard conditions, modulated by the same parameter  $r$  as a result of the environment. Old SOM respiration can be expressed as:

$$R_{\text{SOM}}^{\text{O}} = r k_2 O \quad (10)$$

NEP is the difference between tree and understorey NPP and the heterotrophic respiration from young and old SOM:

$$\text{NEP} = \text{NPP} + \text{NPP}_{\text{und}} - R_{\text{SOM}}^{\text{Y}} - R_{\text{SOM}}^{\text{O}} \quad (11)$$

**Model fitting procedure.** The combined model was implemented in Fortran 95, calibrated independently for each chronosequence on measurements available for a limited number of ages and used to estimate C fluxes at every age in the chronosequence. The procedure made it possible to compute average fluxes over the entire rotation without the risks coming from the limited sample size. In contrast with more empirical equations, such a process-based model can represent coherently and at the same time all of the main C-cycle variables that are amenable to direct measurement. The model was therefore calibrated so as best to represent the values of annual fluxes (NEP and GPP) and C stocks ( $C_{\text{F}}$ ,  $C_{\text{T}}$ ,  $C_{\text{W}}$ , total SOM) measured in individual stands of the chronosequence. The ability of the model to represent all these variables at the same time increased the confidence in model estimates.

To include these non-commensurate sources of information in the calibration process, the multi-objective global optimization approach described in ref. 40 was adopted. Before model calibration, each variable was normalized by its mean and variance, so as to achieve the conditions of zero mean and constant variance among variables, which is a pre-condition for the application of the overall Maximum Likelihood Estimator as an objective function.

A total of seven model parameters ( $f_{\text{tot}}$ ,  $f_{\text{tot}}^{\text{und}}$ ,  $A_{0.5}$ ,  $\gamma_r$ ,  $m$ ,  $h$ ,  $r$ ), plus three initial values of state variables ( $C_{\text{F}}$ ,  $Y$ ,  $O$ ), were estimated for each chronosequence, leaving a number of degrees of freedom ranging between 9 and 21, depending on the chronosequence considered. All other parameters and input variables were derived from direct field measurements. Overall, the model explained 91% of the variability in C stocks and fluxes within each chronosequence.

**Computation of average C fluxes in literature chronosequences.** If not already available, flux integrals over the entire rotation were obtained by fitting onto flux data the empirical equation proposed by ref. 9:

$$\text{NEP} = -a_1 + a_2 \exp\{-0.5[\ln(A/a_3)/a_4]^2\} \quad (12)$$

Alternatively, the empirical equation proposed by ref. 21 was fitted onto total ecosystem C data:

$$C_{\text{eco}} = b_1 + [b_2 \exp(-b_3 A)] + [b_4 A / (A + b_5)] \quad (13)$$

and annual NEP computed as the difference in ecosystem C between subsequent years. The two empirical models were fitted on experimental data with the NLIN procedure in the SAS 9.00 statistical package (SAS Institute). Average NEP over the rotation was computed as the mean of annual values between age zero and the maximum age in the chronosequence. In just one case<sup>22</sup>, because of the limited sample size, average NEP was estimated from the difference in ecosystem C between the newly regenerated and the old stand. Although its omission does

not have any appreciable effects on the results, this *Nothofagus* chronosequence has been included in the analysis because it is one of the few broadleaved forests and the only one from the Southern Hemisphere.

Annual GPP values were also integrated over the entire rotation, using the same function presented in equation (12).  $\text{RE}_{\text{av}}$  was computed as the difference between  $\text{GPP}_{\text{av}}$  and  $\text{NEP}_{\text{av}}$ . A detailed description of data type and integration procedures is presented in Supplementary Table 1 (see Supplementary Information).

**Computation of N wet deposition.** Estimates of N wet deposition in 1990 for sites in western Europe and the conterminous USA were derived from recently published gridded maps with  $0.5^\circ \times 0.5^\circ$  resolution derived from interpolated (krieger) ground data<sup>14</sup> (available at <http://www.daac.ornl.gov>), referring to the nearest node in the map (see Supplementary Fig. 1). Total wet deposition was computed as the sum of aqueous  $\text{NO}_3^-$  and  $\text{NH}_4^+$  fields, which were available for both regions. An estimate of total (modelled) N deposition was obtained as the sum of wet deposition and of the fields for deposition of  $\text{NO}_2$ ,  $\text{NH}_4$ ,  $\text{HNO}_3$  and  $\text{NO}_3^-$ . In the case of Europe, because only the sum of nitric acid and particulate nitrate was measured, the relative fields represent end-members assuming only one species<sup>14</sup> and we took the average value. In the case of the US data set,  $\text{NO}_2$  deposition rates were not available and their contribution to total N deposition was estimated from a regression of European values.

Additional data for 1993 for the rest of the globe were derived from model simulations<sup>5,41</sup>; estimates of wet N deposition were then derived from modelled values of total N deposition, based on a correlation of values from Western Europe in the previous data set (see Supplementary Fig. 2). The same correction factor was used in the comparison with N fertilization rates in manipulation experiments.

**Statistical analyses.** All statistical analyses were carried out using the SAS 9.00 statistical package (SAS Institute).

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# Nitrogen saturation and net ecosystem production

Arising from: F. Magnani *et al.* *Nature* **447**, 848–850 (2007)

Magnani *et al.*<sup>1</sup> found that net carbon (C) sequestration of temperate and boreal forests is clearly driven by nitrogen (N) deposition. From the positive relationship between average net ecosystem production (NEP) and wet N deposition, the authors further conclude that “no signs of N saturation were apparent” in the studied forests and that this is “casting doubts on the risk of widespread ecosystem nitrogen saturation”. Nitrogen additions can clearly alter net ecosystem production, but net ecosystem production cannot be used as an indicator of N saturation.

Nitrogen saturation implies a change in N cycling from a closed internal cycle to an open cycle<sup>2</sup> where excess N is leached and/or emitted from the forest ecosystem. These changes in forest ecosystem functioning have been extensively documented<sup>3,4</sup>. Examples from literature lead us to suggest that some of the forest ecosystems discussed in the concerned article might be N saturated, irrespective of the increased net ecosystem production. Evidence for N saturation has been observed in forest ecosystems subject to N deposition levels similar to the relatively low deposition range reported in the concerned article<sup>1</sup> (that is, less than 10 kg N ha<sup>-1</sup> yr<sup>-1</sup> wet deposition), including considerable nitrate loss (up to 10 kg N ha<sup>-1</sup> yr<sup>-1</sup>) through runoff or seepage water<sup>5–7</sup> and elevated emissions of NO and N<sub>2</sub>O<sup>8</sup>. Because Magnani *et al.*<sup>1</sup> did not measure any of these pathways of N loss, they cannot rule out N saturation in the studied forest ecosystems.

The demonstrated relationship between N deposition and C sequestration is an important finding, consistent with other literature<sup>9</sup>. In our opinion, however, Magnani *et al.*<sup>1</sup> demonstrate an incorrect view on the phenomenon of N saturation and, in doing so, greatly ignore the effect of N deposition and saturation on soil acidification, groundwater and surface water quality, biodiversity, and ecosystem services other than C sequestration. Because the data presented by Magnani *et al.*<sup>1</sup> do not allow an evaluation of the N saturation status of the studied forests, the expressed “doubts on the risk of widespread ecosystem nitrogen saturation” are not substantiated. At the moment, N saturation of forest ecosystems is probably not yet a widespread problem on a global scale, but it is surely a widespread problem in densely populated and more industrialized regions<sup>4,7</sup>. From the Europe-covering IFEF (Indicators of Forest Ecosystem Functioning) and Level-II (UN-ECE/EC intensive monitoring plots) databases<sup>10,11</sup>, it can be deduced that more than 25% of the European forests included in these databases are N saturated (considering the

nitrate seepage flux as indicator and 5 kg (357 mol) N ha<sup>-1</sup> yr<sup>-1</sup> as a threshold value of N saturation). Furthermore, from a large number of sites in the northeastern United States<sup>4</sup>, N saturation was indicated as a frequently occurring phenomenon. As substantial increases in global N emissions are predicted for the coming 50 yr<sup>12</sup>, the potential risk of widespread N saturation of forest ecosystems in the long term cannot be denied.

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Received 20 July; accepted 30 October 2007.

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doi:10.1038/nature06578

## Ecologically implausible carbon response?

Arising from: F. Magnani *et al.* *Nature* **447**, 848–850 (2007)

Magnani *et al.*<sup>1</sup> present a very strong correlation between mean lifetime net ecosystem production (NEP, defined as the net rate of carbon (C) accumulation in ecosystems<sup>2</sup>) and wet nitrogen (N) deposition. For their data in the range 4.9–9.8 kg N ha<sup>-1</sup> yr<sup>-1</sup>, on which the correlation largely depends, the response is approximately 725 kg C per kg N in wet deposition. According to the authors, the maximum N wet deposition level of 9.8 kg N ha<sup>-1</sup> yr<sup>-1</sup> is equivalent to a total deposition of 15 kg N ha<sup>-1</sup> yr<sup>-1</sup>, implying a net sequestration near 470 kg C per kg N of total deposition. We question the ecological plausibility of the relationship and show, from a

multi-factor analysis of European forest measurements, how interactions with site productivity and environment imply a much smaller NEP response to N deposition.

The C response to N deposition is restricted by the C:N stoichiometry of the forest ecosystem compartments. The implied NEP response of 470 kg C per kg N would require that the fate of the deposited nitrogen was exclusively in stem wood, which is the only carbon sink with a C:N ratio of this magnitude. This is unreasonable because N-limited forest stands, as suggested<sup>1</sup>, invest primarily in roots<sup>3</sup>, with C:N ratios near 50–100. The impossibility of near-total

**Table 1 | Multivariate regression results at stand level and individual tree level****a Results at stand level for N sensitive plots with parameter estimates**

Tree species	Site productivity*	Age†	SDI‡	N deposition§	Drought	Temperature change¶
All plots						
Norway spruce	0.054	-0.005	-	0.020#	-	0.524
Scots pine	-	-0.017	-	0.010	-0.0032	-
Sensitive plots						
Norway spruce	0.039	-0.004	-	0.022	-	0.32
Scots pine	-	-0.017	0.001	0.013	-0.002	-

**b Results at individual tree level with parameter estimates for the main influencing factors included**

Tree species	BAL☆	SDI‡	C:N <sub>soil</sub> **	N deposition§	Temperature ††	Temperature change¶
Norway spruce	-0.39	-0.00056	-0.023	0.013	-	-
Scots pine	-0.29	-0.00066	-	0.015	0.053	-
Common beech	-0.16	-	-	0.012	-	0.064
Oak	-0.38	-0.00062	-	0.013	0.080	-

Multivariate regression results indicating the relative change in stem volume growth per unit change in influencing factor (for example, a value of 0.013 for N deposition implies an increase in stem growth of 1.3% for each additional 1 kg ha<sup>-1</sup> yr<sup>-1</sup> of N deposition). Note that a dash (-) implies that the effect was insignificant ( $P > 0.05$ ). Sensitive plots are plots with a C:N ratio above 25.

\* Site productivity is a variable (m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>) derived from selected European site index curves, with input variables being age and top height.

† Stand age (yr).

‡ SDI, stand density index (number of trees per ha).

§ N deposition is total N deposition (unit change: kg ha<sup>-1</sup> yr<sup>-1</sup>).

|| Drought is a variable describing drought given as a relative value (unit change: %) to the normal (30-yr mean) drought stress at each site.

¶ The temperature difference during the growing period compared with the 30-yr average temperature (unit change: °C).

# Results from a linear regression; in the multivariate analysis the coefficient was just not significant at  $P < 0.05$ .

☆ BAL is basal area of larger trees, which affects tree competition (m<sup>2</sup> ha<sup>-1</sup>).

\*\* C:N<sub>soil</sub> is the C:N ratio of the mineral topsoil (0–30 cm).

†† Temperature is average yearly temperature during the investigation period 1993–2000 (°C).

storage of deposited N in stem wood follows also from the expected N leaching rates, varying between 10–50% of the N input in a range of 10–25 kg N ha<sup>-1</sup> yr<sup>-1</sup> (refs 4, 5), which is the likely range for total N deposition at the plots of Magnani *et al.*<sup>1</sup> where the high C:N response was found (that is, their European sites where wet N deposition was estimated at 4.9–9.8 kg N ha<sup>-1</sup> yr<sup>-1</sup>). This total N deposition range follows from an application of the EMEP (European Monitoring and Evaluation Programme of the Long-range Transmission of Air Pollutants) model, used in the NITROEUROPE project, for the year 2000 to the sites of Magnani *et al.*<sup>1</sup> Using this model, the estimates of which are in close agreement with measured atmospheric N deposition at forest sites<sup>6</sup>, we found that total N deposition at the sites of Magnani *et al.*<sup>1</sup> is 2–7 times greater than wet deposition. This analysis implies a relationship of approximately 175 kg C per kg N in the mentioned total N deposition range.

However, even this lower response is unlikely. <sup>15</sup>N-labelled tracer experiments in temperate forests indicate that N retention hardly occurs in stem wood but mainly in the soil<sup>7</sup>. Considering the fate of N and the ranges in C:N ratios in forest ecosystem compartments, this implies a carbon response near 50 kg C per kg N in forest ecosystems<sup>7,8</sup>. Even though the above-ground C sequestration may be underestimated by Nadelhoffer *et al.*<sup>7</sup>, owing to neglecting the effect of direct foliar uptake<sup>9,10</sup>, this effect is likely to be small, as above-ground foliar N uptake is generally less than 5 kg N ha<sup>-1</sup> yr<sup>-1</sup> (ref. 11), whereas below-ground uptake is generally more than 50 kg N ha<sup>-1</sup> yr<sup>-1</sup>. Furthermore, similar results are found in long-term (15–30 yr) nitrogen-fertilizer trials at rates of nitrogen addition below 50 kg N ha<sup>-1</sup> yr<sup>-1</sup> (refs 12, 13) and in process-based model simulations<sup>14</sup>. The reason for the extremely high influence of N deposition on NEP suggested by Magnani *et al.*<sup>1</sup> is probably due to the contribution of other factors—which co-vary with wet N deposition—to the derived relationship. The authors filtered out the effects of age and investigated the separate effect of temperature but they aggregated all tree species and site characteristics, such as site fertility and stand density, into one relationship.

We carried out a multi-factor analysis of measured forest growth data at nearly 400 intensively monitored forest plots in Europe, including Norway spruce, Scots pine, common beech and oak. The influence of nitrogen and acid deposition was considered by using values during the growth period (1993–2000), whereas the impacts of temperature, precipitation and drought were addressed by taking the

deviation of these climatic parameters in the growth period (1993–2000) from the 30-yr mean. We simultaneously accounted for site factors influencing measured tree growth, including site productivity, stand age and stand density. We also applied a multi-factor analysis with measured basal-area increment of each individual tree as responding factor. The influencing factors used in this study and the results of the multivariate analyses at stand and individual tree level are shown in Table 1. The approach at tree level indicated a 1.2–1.5% increase in basal-area increment, depending on tree species, in response to 1 kg of N ha<sup>-1</sup> yr<sup>-1</sup>. The approach at stand level indicated only a significant response of Norway spruce and Scots pine to N with roughly a 1–2% increase in volume growth in response to 1 kg of N ha<sup>-1</sup> yr<sup>-1</sup>, depending on the C:N ratio of the plots. We recalculated these responses in terms of C sequestration by multiplying the mean measured volume growth at each stand with the estimated growth increase and the mean wood density of each tree species, assuming a C content of 50%. The results of our analyses at both tree and stand level indicate a response of trees between approximately 20–40 kg C per kg N. Additionally, results of long-term nitrogen addition experiments indicate soil responses of 10–30 kg C per kg N<sup>12,13,15</sup>. Thus, the total NEP response would be about 30–70 kg C per kg N, which is much smaller than that estimated by Magnani *et al.*<sup>1</sup>

## METHODS

The multivariate regression at stand level was carried out by a backward stepwise method, where the model was reduced step-by-step by removing nonsignificant effects. The results of the hypothesis testing of the effects are based on partial *F*-tests.

The multivariate regression analysis at tree level was carried out by using tree size and tree competition variables on tree level and site factors and environmental factors on plot level, including plot as a random effect and applying the restricted maximum likelihood (REML) method for parameter estimation. Parameters in the model, which exhibited significant ( $P < 0.05$ ) coefficients and behaved according to their known impacts, are included in Table 1b. We accounted for correlations, such as those between climatic parameters and N deposition (for example, we found a quadratic relation between N deposition and temperature;  $R^2 = 0.62$ ).

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Received 23 July; accepted 16 November 2007.

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doi:10.1038/nature06579

## Magnani *et al.* reply

Replying to: A. De Schrijver *et al.* *Nature* **451**, doi:10.1038/nature06578; W. de Vries *et al.* *Nature* **451**, doi:10.1038/nature06579 (2008)

Nitrogen (N) deposition alters ecosystem function in several ways, with important effects on N leaching and water quality, as well as on interspecific competition and biodiversity. These changes have been attributed to ecosystem N saturation, defined as the alleviation of N limitations on rates of biological function<sup>1</sup>. After an initial fertilization effect, N saturation has also been suggested to reduce plant function and growth<sup>2</sup>, eventually leading to forest dieback. Although our observation of a substantial positive effect of N deposition on forest carbon (C) sequestration<sup>3</sup> does not imply the absence of nitrate losses or other negative effects, as rightly stressed by De Schrijver *et al.*<sup>4</sup>, the sustained response observed demonstrates that the fear of a generalized forest decline in response to N fertilization could be overstated, at least within the rather broad N deposition range explored in our analysis. The nature of the observed response of forest C sequestration to N deposition, however, has been questioned outright by de Vries *et al.*<sup>5</sup>, who suggested that it could be an artefact resulting from the covariation between N deposition and other environmental variables. The arguments proposed against an overwhelming N effect, however, do not seem to stand up to close scrutiny.

We agree that ecosystem gross primary production (GPP) and plant growth are, to a large extent, controlled by local climate, drought and fertility (that is, N mineralization associated with soil organic matter decomposition), although fertility could be itself influenced by current and past N deposition<sup>6</sup>. However, the same environmental factors would modulate in parallel ecosystem respiration, and as a result do not seem to affect net ecosystem production (NEP), which is the difference between GPP and ecosystem respiration and is the subject of our analysis<sup>3</sup>. Both components of NEP seem to be also affected by N deposition, but in opposite directions: apart from the positive effects on plant growth considered by de Vries *et al.*<sup>5</sup>, respiration is known to be significantly reduced by N fertilization, as demonstrated by manipulation experiments<sup>7,8</sup> as well as regional transect studies<sup>9</sup>. The combined effect at the ecosystem level is largely missed when focusing on tree growth alone.

The question remains of the magnitude of the observed response to N deposition. Assuming a linear relationship between NEP and N

deposition, a slope of  $445 \pm 38$  kg C per kg N of wet N deposition can be inferred from our entire data set ( $n = 20$ , rather than the subsample of 8 data points in the analysis by de Vries *et al.*<sup>5</sup>). If we assume, rather conservatively, that wet deposition constitutes 40–50% of total N deposition<sup>10</sup>, this would imply a NEP sensitivity to total N deposition of approximately 175–225 kg C per kg N, which is consistent with the stoichiometry of plant tissues and soil organic matter. Although it is true that fine roots account for a significant fraction of forest growth, it should be noted that one of the main effects of increased N availability is an increased allocation to woody tissues (with a high C:N ratio of up to 500:1) away from fine roots<sup>11</sup>. This mechanism could indeed represent an important component of the observed response to N deposition.

Far from implausible, a 200:1 sensitivity is nevertheless higher than suggested by long-term forest fertilization experiments<sup>12</sup>. Potential problems with N manipulation studies have already been discussed<sup>13</sup>. In particular, they overlook the role of canopy N uptake, which enables plants to absorb a relevant fraction of incoming N without any competition from soil microbes. Canopy N uptake amounts to up to 70% of N deposition, providing as much as one-third of tree N requirements<sup>9,14,15</sup>. The critical comparison of results from ecosystem manipulation and observational studies could be providing a rare, unforeseen insight into the key factors controlling C–N relations in forest ecosystems.

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doi:10.1038/nature06580