

RAPID COMMUNICATION

Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration

MARK A. SUTTON*, DAVID SIMPSON†‡, PETER E. LEVY*, ROGNVALD I. SMITH*, STEFAN REIS*, MARCEL VAN OIJEN* and WIM DE VRIES§

*Centre for Ecology and Hydrology, Edinburgh Research Station, Bush Estate, Penicuik, Midlothian EH26 0QB, UK, †Norwegian Meteorological Institute, PO Box 43, Blindern, NO-0313 Oslo, Norway, ‡Chalmers University of Technology, SE-412 96 Göteborg, Sweden, §Alterra, Wageningen University and Research Centre, PO Box 47, 6700 AA Wageningen, The Netherlands

Abstract

In a recent study, Magnani *et al.* report how atmospheric nitrogen deposition drives stand-lifetime net ecosystem productivity (NEP_{av}) for midlatitude forests, with an extremely high C to N response (725 kg C kg⁻¹ wet-deposited N for their European sites). We present here a re-analysis of these data, which suggests a much smaller C:N response for total N inputs. Accounting for dry, as well as wet N deposition reduces the C:N response to 177:1. However, if covariance with intersite climatological differences is accounted for, the actual C:N response in this dataset may be <70:1. We then use a model analysis of 22 European forest stands to simulate the findings of Magnani *et al.* Multisite regression of simulated NEP_{av} vs. total N deposition reproduces a high C:N response (149:1). However, once the effects of intersite climatological differences are accounted for, the value is again found to be much smaller, pointing to a real C:N response of about 50–75:1.

Keywords: atmospheric deposition models, biogeochemical models, carbon sequestration, chronosequences, forest growth, greenhouse gas budgets, net ecosystem productivity, nitrogen deposition, regression analysis, uncertainty

Received 14 November 2007; revised version received 8 February 2008 and accepted 1 February 2008

Introduction

A major debate is emerging that is concerned with the effect of atmospheric nitrogen deposition (N_{dep}) on net carbon uptake by forest stands. In a recent paper, Magnani *et al.* (2007) made an analysis of CO₂ fluxes using forest chronosequences in Europe, Asia and North America to show how net ecosystem productivity (NEP) varies strongly through the life of a rotation: stands change from being carbon sources to carbon sinks within around 10 years of planting, while sink strength is strongest at 20–40 years, thereafter slightly reducing in mature stands. To account for these temporal differences when looking for relationships with environmental conditions, Magnani *et al.* (2007) calculated the average NEP over a stand's lifetime (NEP_{av}), as well as its components, gross primary productivity

(GPP_{av}) and ecosystem respiration (RE_{av}). Applying a regression approach to their multisite dataset, they found that GPP_{av} and RE_{av} responded similarly to temperature ($R^2 = 0.92$ in each case), tending to cancel out the effect of temperature on NEP_{av} , so that the latter were less well correlated ($R^2 = 0.41$, their Fig. 3c). By contrast, there was a substantial effect of N_{dep} on NEP_{av} (their Fig. 3d). Magnani *et al.* (2007) concluded that the NEP_{av} response was 'overwhelmingly driven' by N_{dep} , while the actual NEP_{av} relationship implicit in their interpretation was close to 400 kg C sequestered for every 1 kg of nitrogen wet-deposited from the atmosphere (see Brahic, 2007 for a reflection of the authors' announcement to the press). In fact, Magnani *et al.* (2007) highlighted that the NEP_{av} response to N_{dep} was nonlinear, increasing more strongly at higher N_{dep} , which they attributed to a larger fraction of N_{dep} being allocated to plants as microbial N demand becomes saturated. For a linear upper part of the relationship (which represented all the European sites and

Correspondence: Mark A. Sutton, tel. +44 131 443 4343, fax +44 131 445 3943, e-mail: ms@ceh.ac.uk

determined the overall correlation reported by Magnani *et al.* 2007), the C:N response in their data was actually 726:1. Such a finding differs markedly from other estimates (Hogberg, 2007; de Vries *et al.*, 2008), and demands careful analysis. Although authors on both sides of the debate agree that nitrogen is a key driver, the argument focuses on what should be the correct value of the NEP_{av} response to N_{dep} .

The quantitative relationships are important for both scientists and policy makers. If the C:N response were as high as Magnani *et al.* seemed to imply, the counteracting effects of N on greenhouse gas budgets (e.g. through nitrous oxide and methane fluxes or via ozone effects on forest growth) would tend to be smaller in comparison (Sutton *et al.*, 2007). This might lessen the incentive to reduce N emissions, even though abatement strategies must also consider the wide range of adverse effects of nitrogen (see de Schrijver *et al.*, 2008), such as on terrestrial biodiversity, health impacts of air pollution and on inland and marine water quality.

Generalists may also consider the Magnani *et al.* relationship useful to scale up the implications (e.g. Brahic, 2007). Given the potential relevance, it is important to sound a note of caution. The dangers of a simple extrapolation of the Magnani *et al.* results may be illustrated by the following example. In the UK, total N_{dep} to UK forests is estimated at 68 Gg yr^{-1} (NEGTAP, 2001; updated for 2000–2005; R. I. Smith, personal communication). With a C:N response of 400:1, it might be suggested that N_{dep} accounts for $\sim 27\,200 \text{ Gg C yr}^{-1}$ taken up by UK forests. However, even if roughly half of NEP_{av} is exported from forests, this figure remains unfeasibly large compared with the total estimated UK forest C sequestration (4292 Gg C for 2005, accounting for plantings since 1920, Thomson & van Oijen, 2007). It is clear that a more detailed approach is needed, matched with careful scrutiny of the Magnani *et al.* conclusions.

The first reaction to Magnani *et al.* (2007) was published simultaneously. Hogberg (2007) strongly supported the view that nitrogen should increase carbon sequestration in forests, but suggested that the C:N response had probably been overestimated by Magnani *et al.* Drawing on a recent review, Hogberg estimated that 1 kg of nitrogen was likely to sequester around 30 kg C in the trees and an additional 10 kg C in the soil, giving an overall C:N response of 40, an order of magnitude smaller than that implied by Magnani *et al.*

The findings were further questioned by de Vries *et al.* (2008). They argued how the stoichiometry of the forest system would make it difficult to generate such high numbers and presented new results from an extensive analysis of European forest stands, including all major factors affecting forest growth, which showed a C:N response for the trees to atmospheric N deposition of

approximately 20–40:1. Allowing for a further contribution to the C:N response of 10–30:1 in the soil, de Vries *et al.* (2008) therefore proposed that the overall response would be an NEP of around 30–70 kg C for every 1 kg of atmospheric N deposition. de Vries *et al.* also highlighted a key point of detail in the original analysis that nonspecialists may have missed – strictly speaking, the NEP_{av} response of Magnani *et al.* was only in relation to wet deposition rather than total N deposition, with dry deposition of nitrogen being excluded from their analysis. Magnani *et al.* had considered that the spatial estimates of dry deposition available to them were too uncertain, and therefore focused their analysis only on wet deposition.

In seeking to explain why Magnani *et al.* (2007) had obtained such a high C:N response, de Vries *et al.* (2008) hypothesized that this was an artefact of the regression approach used, due to climatological and other factors confounding the single-factor analysis of N_{dep} vs. NEP_{av} . For example, if temperature were positively correlated with N deposition (as would be expected), then the real C:N response in the data of Magnani *et al.* would be somewhat smaller.

In the present paper we, therefore, take the debate further by re-examining the data published by Magnani *et al.* We consider two issues affecting the suggested carbon response to N deposition.

1. The total N deposition to the study sites. We estimate the values of wet and dry deposition and consider the importance of uncertainty in the total N deposition values.
2. The potential for climatological interactions with NEP_{av} to affect the reported C:N response. We combine our estimates of total N deposition with the NEP_{av} data of Magnani *et al.* and other climatological parameters to investigate possible interactions.

Having accounted for total N deposition, we find the evidence of a substantial remaining climatological effect on NEP_{av} , indicating that the real C:N response is much smaller than inferred by Magnani *et al.* To further investigate this, we therefore compare the results of our re-analysis with process-based models. Using a multi-site application of a C–N forest model and regression analysis, we illustrate how it is possible to reproduce the high C:N response reported by Magnani *et al.*, while the underlying causal C:N response is much smaller. In demonstrating the role of climatological effects, our analysis shows that, while N_{dep} remains an important driver of NEP_{av} , the dataset of Magnani *et al.* (2007) does not support their conclusion that NEP_{av} is ‘overwhelmingly driven by nitrogen deposition.’

Methods

In the first stage we sought to relate the Magnani *et al.* (2007) NEP_{av} values to independent estimates of wet and dry N_{dep} . Although their dataset included sites from around the globe, the observed response between NEP_{av} and N_{dep} is entirely dependent on the seven European sites used in the analysis. We, therefore, focused our attention on these sites. It should be noted that the Magnani *et al.* (2007) precipitation and N_{dep} results are not measurements obtained at the forest study sites in question, but rather the results of a large-scale interpolation, based in Europe on measurements from the European Monitoring & Evaluation Programme (EMEP) network (Holland *et al.*, 2005). The data used were rather old (1978–1994), and the quality assurance for this network was rather inhomogenous over those years. The network was also rather sparse in many areas, so that the sites of Magnani *et al.* (2007) are in some cases hundreds of kilometers away from the nearest EMEP station. Precipitation and nitrogen deposition have very large spatial variability, and so the N_{dep} values used by Magnani *et al.* should not be taken as ‘measured,’ but rather estimated, and with a wide uncertainty range.

These uncertainties are even larger for dry deposition, which was why Magnani *et al.* excluded it from their analysis. Although not perfect, models allow an estimate of both dry and wet deposition components. To provide spatially coherent estimates across Europe, we, therefore, estimated wet and dry deposition for 2000 using the EMEP unified model (Simpson *et al.*, 2003, 2006a, www.emep.int), which is an Eulerian system quantifying emissions-dispersion-chemistry-deposition at 50 km resolution, driven by 3-hourly meteorology and providing ecosystem-specific dry deposition. Comparison of modeled data to EMEP observations from 1990 and 2000, or International Cooperative Programme (ICP)-forest data for 1997 and 2000, shows that air concentrations and wet depositions of total nitrate and ammonia are reproduced within 20–30% on average (Simpson *et al.*, 2006b). Detailed comparison against dry and wet deposition for the forest site Speulderbos in the Netherlands (Simpson *et al.*, 2006a) showed agreement to within 10% for total deposition, with very close agreement for the wet and dry components of oxidized and reduced nitrogen. As an indication of uncertainty, we compared the EMEP estimates with independent measurements of wet N_{dep} which were available at two of the study sites in Germany (Mund, 2004; Site 1, Hainich; Site 2, Dün; site numbers according to Magnani *et al.*, 2007). In addition, for the UK study site (Site 7, Harwood), we compared the results with the high-resolution NEG-TAP (National Expert Group on Transboundary Air Pollution) model to estimate

wet and dry N_{dep} for the four surrounding 5 km grid squares. The NEG-TAP model provides independent estimates of orographically enhanced measured wet N_{dep} from 38 UK sites, with dry N_{dep} calculated from resistance modeling using gas/aerosol concentrations derived from high-resolution national monitoring (Smith *et al.*, 2000; NEG-TAP, 2001; Sutton *et al.*, 2001).

It is worth noting that Magnani *et al.* (2007) focused their analysis of climatological interactions with NEP_{av} on mean annual temperature and annual precipitation. While both these terms help distinguish major climatological differences, they can mask important nonlinear responses to thermal conditions and water input into ecosystems. For this reason, we also related the results of Magnani *et al.* (2007) to other climatological parameters. In this paper, we examine the response of their NEP_{av} estimates to annual growing degree days above 5 °C (GDD5) and to the ratio of actual evapotranspiration to potential evapotranspiration (AET/PET). The estimates of GDD5 and AET/PET were specified at 0.5° resolution from a database made available by the Potsdam Institute for Climate Impacts Research (Sutton *et al.*, 2001), using the BIOME model (Prentice *et al.*, 1992; Cramer, 2002).

Based on our recalculation of total N_{dep} at the sites, we compared the NEP_{av} responses of Magnani *et al.* (2007) with three process-based ecosystem models: the Edinburgh Forest Model (EFM, Thornley, 1991; Milne & van Oijen, 2005), Biome-BGC (v4.1, Running & Gower, 1991) and the CENTURY model (v4, Parton *et al.*, 1987). We first applied all three models for a single northern latitude forest stand, through an entire rotation (100 years), using the same inputs as Levy *et al.* (2004), but investigated the response to smaller values of total N_{dep} . The purpose of this was to quantify the modeled C:N response of NEP_{av} vs. total N_{dep} , without interference from intersite differences. Secondly, we applied the EFM model to 22 forest stands across Europe (EU RECOGNITION project, van Oijen *et al.*, 2008), using detailed site-level information, including: site-specific soil conditions, planting year, planting density, time-series of tree thinning, weather, total N_{dep} . For this part of the analysis, total N_{dep} at each of the RECOGNITION forest stands was calculated as the mean over the lifetime of each stand (33–125 years).

Results and discussion

Deposition estimates

Using the EMEP estimates, we find a broadly similar NEP_{av} to wet N_{dep} response to Magnani *et al.* (2007), although the nonlinear response highlighted by those

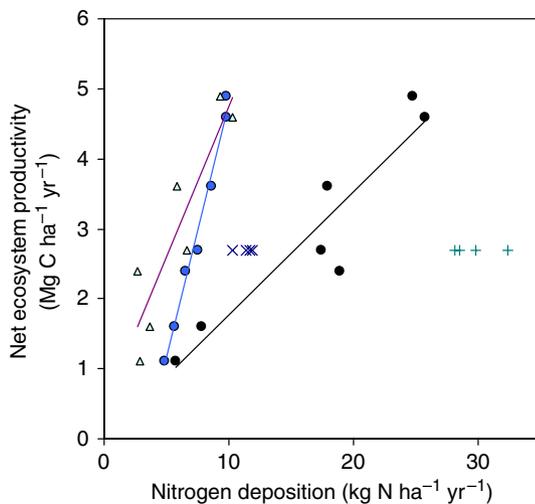


Fig. 1 Relationships between average net ecosystem productivity (NEP_{av}) of midlatitude forests and different estimates of atmospheric nitrogen deposition (N_{dep}). Measured NEP_{av} vs. wet deposition estimates of Magnani *et al.* (2007) (●, C:N = 726:1) are compared with EMEP model estimates of wet deposition (▲, C:N = 428:1) and total N deposition (●, C:N = 177:1) for 2000, and with NEGTAP high-resolution wet (×) and total (+) N_{dep} to the four 5 km grid squares surrounding Site 7 of Magnani *et al.*

authors disappears (Fig. 1). The impression is that the nonlinearity that Magnani *et al.* described was an artefact of uncertainties in the wet deposition dataset, especially given the small number of measurement points on which it depended. It may also be noted that there was no significant correlation for the Magnani *et al.* non-European sites, where their wet N_{dep} estimates were less than $2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (their Fig. 3d). Overall, using the EMEP wet N_{dep} estimates for 2000, the relationship is adequately described by a linear C:N response of 428:1 ($R^2 = 0.82$). In reacting to points made by de Vries *et al.* (2008), and to an earlier draft of the present paper, Magnani *et al.* (2008) now appear to accept our argument in this respect.

Figure 1 also shows total N_{dep} at each site as being between two and seven times larger than wet N_{dep} , demonstrating how the relative contribution of dry N_{dep} is very different between sites. These differences are expected, and reflect the different patterns of emissions, reactive nitrogen air concentrations and precipitation across Europe.

Accounting for total N_{dep} , the NEP_{av} response reduces to 177:1 ($R^2 = 0.88$). While we calculated this response using EMEP total N_{dep} for 2000, it is worth noting that past deposition was larger, and applying EMEP total N_{dep} values for 1990 [which would be more consistent with the estimates of Holland *et al.* (2005)], would give a lower C:N response of 126:1 ($R^2 = 0.87$).

The uncertainty in both the interpolated wet N_{dep} values of Holland *et al.* (2005) and the EMEP model values is illustrated by the independent measurements of bulk wet deposition reported by Mund (2004) for the Magnani *et al.* sites 1 and 2. In Fig. 1, these two sites have $NEP_{av} = 4.9$ and $4.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively, with both Magnani *et al.* (2007) and EMEP model (2000) estimating bulk wet deposition at 9.3 – $10.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. However, the site measured bulk wet N_{dep} is estimated at $12.8 \pm 3.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Mund, 2004), suggesting a potential underestimation of wet N_{dep} by both models at these sites by 20–30%. For the comparison with the NEGTAP model for Site 7 in the UK, the scatter in the four 5 km squares surrounding the site demonstrates the importance of local variability, especially for dry deposition. Both wet and dry depositions are larger than estimated by the Holland *et al.* (2005) interpolation and the EMEP model. If a linear response were applied using the NEGTAP estimates of total N_{dep} , the implied NEP_{av} relationship would reduce to a C:N response of 91:1. These different estimates are important to highlight the uncertainty in quantifying the components of N_{dep} , and how this uncertainty propagates to estimates of the NEP_{av} response to N_{dep} . However, while recognizing these uncertainties, the comparisons show that it is essential to quantify both wet and dry N_{dep} in order to derive sound values of the NEP_{av} response. For simplicity, in the following analyses we report only the results using EMEP values for 2000. If the EMEP 1990 or NEGTAP values were used, the derived estimates of C:N response would reduce accordingly.

Climatological interactions

Having accounted for total N_{dep} , the corrected C:N response of Magnani *et al.* (2007) still remains larger than expected. We were therefore interested to see whether there were other interactions that would contribute to the apparent NEP_{av} :total N_{dep} response. A key point of interest is that Magnani *et al.* (2007) demonstrated a major temperature sensitivity in both GPP_{av} and RE_{av} . As NEP_{av} is simply the difference between these terms, there is no *a priori* reason why there should be no NEP_{av} response to temperature. In fact, although the correlation between NEP_{av} and mean annual temperature reported by Magnani *et al.* ($R^2 = 0.41$) is weaker than that with wet N_{dep} ($R^2 = 0.98$), the relationship between NEP_{av} and temperature remains substantial (accounting for a change of $3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ across the full range of their sites). It is therefore possible that thermal differences between sites explain part of the apparent NEP_{av} response to

total N_{dep} . If the temperature response (Fig. 3c of Magnani *et al.*, 2007) is used to normalize the values of NEP_{av} to 10°C , the C:N response using EMEP total N_{dep} for 2000 reduces from 177:1 to 130:1.

A further example is useful to illustrate the role of climate in affecting NEP_{av} . Figure 2 shows the NEP_{av} results for the same European sites of Magnani *et al.* in relation to the more suitable climatic indicators GDD5 and AET/PET. Of the seven European sites analyzed by Magnani *et al.* (2007), Fig. 2a shows that two of these sites have a substantial moisture deficit (Site 10, Le Bray/Bilos, southwest France; Site 19, Roccarespampiani, Italy). These two sites are shown as clear outliers in an otherwise close relationship between NEP_{av} and GDD5 (Fig. 2b). Excluding these two sites, the relationship gives $R^2 = 0.98$, which is even higher than the relationship between NEP_{av} and total N_{dep} . As a consequence, multiple regression of total N_{dep} and GDD5 vs. NEP_{av} for the remaining sites ($R^2 = 0.99$, $P = 0.012$), assigns the variation first to GDD5. This reduces the estimated NEP_{av} response to N_{dep} (EMEP for 2000) from 177:1 to 68:1. The inclusion of N_{dep} adds little to the relationship, and while the overall multiple regression is significant, the individual effect of N_{dep} is not ($P = 0.38$). Although, in reality, it is not possible to say whether GDD5 or N_{dep} is the main driver, this example again illustrates how climatic interactions can explain the apparently high C:N response reported by Magnani *et al.* (2007).

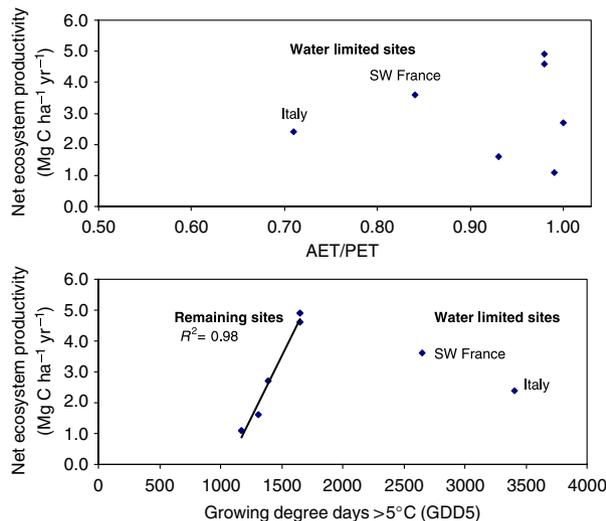


Fig. 2 Relationship between NEP_{av} of Magnani *et al.* (2007) and two climatological variables estimated at 0.5° : (a) actual evapotranspiration/potential evapotranspiration (AET/PET), (b) growing degree days above 5°C (GDD5). The two outlier sites are Site 10 (Le Bray/Bilos, SW France) and Site 19 (Roccarespampiani, Italy) according to the site numbering of Magnani *et al.*

Ecosystem modeling

Having corrected the Magnani *et al.* (2007) NEP_{av} response for total N_{dep} and shown how climatic interactions can give misleadingly high C:N values, we were interested to see how the results compared with process-based models. Figure 3 shows results from the application of EFM, BGC and CENTURY to a single coniferous stand in boreal conditions. Overall, the response of measured NEP_{av} to total N_{dep} fits within the range of the model estimates. Superficially, this might appear to show that the NEP_{av} dataset of Magnani *et al.* (2007) combined with EMEP total N_{dep} for 2000 is broadly consistent with the existing models. However, a closer assessment shows that the NEP_{av} measurements do not show the N saturation effect that is revealed by EFM and CENTURY. For the range of total N_{dep} at the study sites ($5.8\text{--}25.7\text{ kg N ha}^{-1}\text{ yr}^{-1}$, EMEP for 2000), the modeled C:N responses are as follows: EFM, 75:1; CENTURY, 58:1; BCG, 43:1. Each of these is much smaller than the value of 177:1 estimated by combining the Magnani *et al.* (2007) results with the EMEP values (for 2000) of total N_{dep} .

While the model results give a useful indication of expected C:N response, we recognize that models have their own uncertainties, as illustrated by the differences

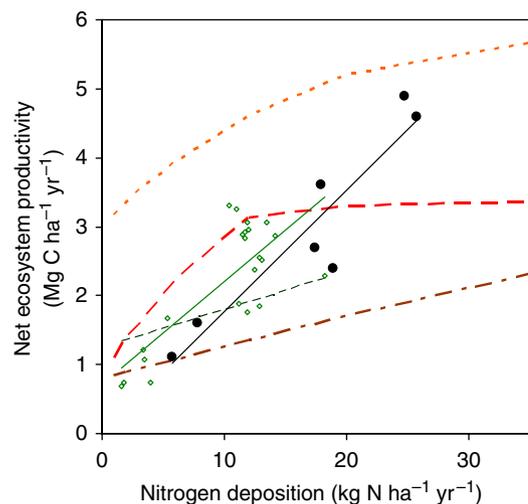


Fig. 3 Comparison of the Magnani *et al.* (2007) average net ecosystem productivity (NEP_{av}) response to total N_{dep} (EMEP for 2000, ●) with the NEP_{av} responses to N_{dep} of three forest models (EFM, CENTURY, BGC) applied to a northern coniferous forest stand (C:N responses: 75:1, 58:1 and 43:1, respectively). The EFM model was also applied to 22 European forest stands (◇) and used to simulate a single-factor analysis of spatial NEP_{av} estimates vs. total N_{dep} (—, C:N = 149:1, $R^2 = 0.60$). Accounting for interactions with temperature and precipitation improves the overall correlation for the 22 sites ($R^2 = 0.81$), and attributes a much smaller response to nitrogen (---, C:N = 54:1).

between EFM, BGC and CENTURY. Nevertheless, modeling also provides a useful tool to simulate the interactions between climate, N_{dep} and NEP_{av} . In the results of the EFM simulations at 22 European sites, the first point to highlight is that EFM simulates substantial changes in C:N through the lifetime of a forest rotation. Figure 4 shows the change in modeled carbon stock relative to change in nitrogen stock in the trees ($dC_{\text{tree}}/dN_{\text{tree}}$) for an example site (Kemijarvi, Finland) from planting in 1935 to harvest in 2000. The scatter in the graph is a result of temporal interactions between growth and meteorological variability. However, the overall pattern shows that EFM simulates low C:N ratios during stand establishment, while the mature forest has a much lower nitrogen requirement.

Using the modeled NEP_{av} for the stand lifetimes of the 22 forests, we related the EFM results to the modeled total N_{dep} to these forests. Plotted as a single factor regression, using the same approach as Magnani *et al.* (2007), the EFM application showed a very high apparent NEP_{av} response to total N_{dep} (Fig. 4). The C:N response was 149:1 ($R^2 = 0.60$, $P < 0.0001$), which is close to the response of 177:1 for NEP_{av} (Magnani *et al.*, 2007) vs. total N_{dep} (EMEP for 2000). Using the model, however, we see that the high NEP_{av} response is an artefact of the single-factor regression. Multiple regression of the EFM NEP_{av} shows that both temperature and precipitation are significant factors ($P = 0.003$ and 0.02 , respectively). Accounting for these reduces the C:N response to 54:1 ($P = 0.17$), with the multi-factor regression being significant to $P < 0.00001$ ($R^2 = 0.81$).

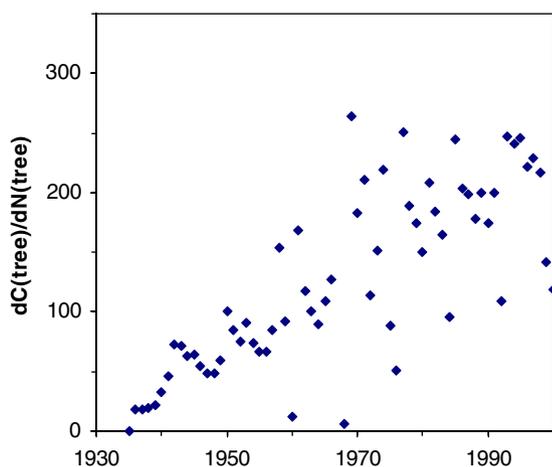


Fig. 4 Relationship between carbon and nitrogen sequestration in coniferous trees through an entire forest rotation for the years 1935–2000, as simulated using the Edinburgh Forest Model (EFM). The data represent annual estimates of $dC_{\text{tree}}/dN_{\text{tree}}$ simulated for actual site conditions of meteorology, soils and forest management for Kemijarvi in Finland.

Hence, regression analysis of the EFM results across 22 European sites is able to simulate the high apparent C:N response reported by Magnani *et al.* (2007), while the actual modeled C:N response is much lower. While noting the qualitative arguments put forward in a recent response by Magnani *et al.* (2008), as well as their acceptance of some of our arguments, our conclusion is that their interpretation of a high C:N response is not supported by the dataset of Magnani *et al.* (2007). As we have shown here, this appears to be an artefact caused by climatological interactions with NEP_{av} . In addition, other effects of intersite differences (such as interactions with soil types between sites) may further reduce the derived C:N response (de Vries *et al.*, 2008). The result is that while N_{dep} remains an important determinant of NEP_{av} , as illustrated by the model responses in Fig. 3, it cannot be concluded that N_{dep} is the ‘overwhelming driver’ of NEP_{av} .

Taking account of the consistency of the EFM reconstruction using the RECOGNITION sites with the dataset of Magnani *et al.* (2007), the clear climatic interaction in the latter (e.g. NEP_{av} with GDD5 and AET/PET), and the uncertainties in total N_{dep} , we arrive at an NEP_{av} response to total N_{dep} which is probably in the region of 50–75:1. Overall, this is not so different from the estimates of Hogberg (2007) and de Vries *et al.* (2008) which were based on the fate of N, pool stoichiometry and measurements of forest growth.

Acknowledgements

This analysis was conducted under the EU NitroEurope Integrated Project (www.nitroeuropa.eu) with support from the ESF Nitrogen in Europe (NinE) program. It synthesizes results from several other projects including the UK NERC-funded GANE program (NER/T/S/2000/00218) and the EU-funded project RECOGNITION (FAIR CT98-4124), as well as the Co-operative Programme for Monitoring and Evaluation of the Long-Range Transmission of Air Pollutants in Europe (EMEP) under the UNECE. Biome-BGC version 4.1 was provided by the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana. Century version 4 was provided by the Natural Resource Ecology Laboratory (NREL) at Colorado State University. The simulations using the EFM and NEG-TAP models were conducted by the Centre for Ecology and Hydrology and those using the EMEP model by the Norwegian Meteorological Institute. We are grateful for the constructive comments of two anonymous referees.

References

- Brahic C (2007) New Scientist.com news service 18:00 13 June 2007. <http://environment.newscientist.com>
- Cramer W (2002) Biome models. In: *Encyclopedia of Global Environmental Change, Volume 2, the Earth System: Biological and Ecological Dimensions of Global Environmental Change*

- (eds Mooney HA, Canadell JG), pp. 166–171. John Wiley & Sons Ltd, Chichester.
- De Schrijver A, Verheyen K, Mertens J, Staelens J, Wuyts K, Muys B (2008) Nitrogen saturation and net ecosystem production. *Nature*, **451**, E1–E1, doi: 10.1038/nature06578.
- De Vries W, Solberg S, Dobbertin M *et al.* (2008) Ecologically implausible carbon response. *Nature*, **451**, E1–E3, doi: 10.1038/nature06579.
- Hogberg P (2007) Nitrogen impact on forest carbon. *Nature*, **447**, 781–782.
- Holland EA, Braswell BH, Sulzman J, Lamarque J-F (2005) Nitrogen deposition onto the United States and western Europe: synthesis of observations and models. *Ecological Applications*, **15**, 38–57.
- Levy PE, Wendler R, van Oijen M, Cannell MGR, Millard P (2004) The effect of nitrogen enrichment on the carbon sink in coniferous forests: uncertainty and sensitivity analyses of three ecosystem models. *Water Air and Soil Pollution: Focus*, **4**, 67–74.
- Magnani F, Mencuccini M, Borghetti M *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–851.
- Magnani F, Mencuccini M, Borghetti M *et al.* (2008) Magnani *et al.* reply to A. De Schrijver *et al.* (2008) and W. de Vries *et al.* (2008). *Nature*, **451**, E3–E4, doi: 10.1038/nature06580.
- Milne R, van Oijen M (2005) A comparison of two modelling studies of environmental effects on carbon stocks across Europe. *Annals of Forest Science*, **62**, 1–13.
- Mund M (2004) *Carbon pools of European beech forests (Fagus sylvatica) under different silvicultural management*. PhD thesis, Georg-August-Universität Göttingen.
- NEGTA (2001) *UK National Expert Group on Transboundary Air Pollution*. Defra, London.
- Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.
- Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.
- Running SW, Gower ST (1991) Forest-BGC, a general-model of forest ecosystem processes for regional applications: 2. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology*, **9**, 147–160.
- Simpson D, Butterbach-Bahl K, Fagerli H, Kesik M, Skiba U, Tang YS (2006a) Deposition and emissions of reactive nitrogen over European forests: a modelling study. *Atmospheric Environment*, **40**, 5712–5726.
- Simpson D, Fagerli H, Hellsten S, Knulst JC, Westling O (2006b) Comparison of modelled and monitored deposition fluxes of sulphur and nitrogen to ICP-forest sites in Europe. *Biogeosciences*, **3**, 337–355.
- Simpson D, Fagerli H, Jonson JE, Tsyro S, Wind P, Tuovinen JP (2003) *The EMEP Unified model. Model description*. EMEP MSCW Report 1/2003, Norwegian Meteorological Institute, Oslo, Norway.
- Smith RL, Fowler D, Sutton MA, Flechard C, Coyle M (2000) Regional estimation of pollutant gas deposition in the UK: model description, sensitivity analyses and outputs. *Atmospheric Environment*, **34**, 3757–3777.
- Sutton MA, Dragosits U, Cramer W (2000) Application of European scale transects in the Terrestrial Ecosystem Research Initiative. In: *Terrestrial Ecosystem Research in Europe: Successes, Challenges and Policy* (eds Sutton MA, Moreno JM, van der Putten W, Struwe S), pp. 189–196. European Commission, Luxembourg EUR, 19375.
- Sutton MA, Nemitz E, Erisman JW *et al.* (2007) Challenges in quantifying biosphere-atmosphere exchange of nitrogen species. *Environmental Pollution*, **150**, 125–139.
- Sutton MA, Tang YS, Dragosits U *et al.* (2001) A spatial analysis of atmospheric ammonia and ammonium in the UK. *The Scientific World*, **1**, 275–286.
- Thomson AM, van Oijen M (eds) (2007) *Inventory and projections of UK emissions by sources and removals by sinks due to land use, land use change and forestry*. Report C03116, Centre for Ecology and Hydrology/DEFRA, London.
- Thornley JHM (1991) A transport-resistance model of forest growth and partitioning. *Annals of Botany*, **68**, 211–226.
- van Oijen M, Ågren GI, Chertov OG, Kellomäki S, Komarov A, Mobbs DC, Murray MB (2008) Evaluation of past and future changes in European forest growth by means of four process-based models. In: *Causes and Consequences of Forest Growth Trends in Europe*, (Chapter 4.4) (eds Kahle HP, Karjalainen T, Schuck A, Ågren GI, Kellomäki S, Mellert KH, Prietzel J, Rehfuss KE, Spiecker H), pp. 183–199. EFI Research Reports, Brill Publ., Lieden.