# RAPID COMMUNICATION

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

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# Abstract

In a recent study, Magnani *et al.* report how atmospheric nitrogen deposition drives stand-lifetime net ecosystem productivity (NEP<sub>av</sub>) for midlatitude forests, with an extremely high C to N response (725 kg C kg<sup>-1</sup> 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<sub>av</sub> 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

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### 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 CO<sub>2</sub> 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<sub>av</sub>), as well as its components, gross primary productivity

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(GPP<sub>av</sub>) and ecosystem respiration (RE<sub>av</sub>). Applying a regression approach to their multisite dataset, they found that GPP<sub>av</sub> and RE<sub>av</sub> responded similarly to temperature ( $R^2 = 0.92$  in each case), tending to cancel out the effect of temperature on NEP<sub>av</sub>, so that the latter were less well correlated ( $R^2 = 0.41$ , their Fig. 3c). By contrast, there was a substantial effect of  $N_{\rm dep}$  on NEP<sub>av</sub> (their Fig. 3d). Magnani et al. (2007) concluded that the NEP<sub>av</sub> response was 'overwhelmingly driven' by N<sub>dep</sub>, while the actual NEP<sub>av</sub> relationship implicit in their interpretation was close to 400 kg C sequestered for every 1kg 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<sub>av</sub> response to N<sub>dep</sub> 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

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<sub>av</sub> response to N<sub>dep</sub>.

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<sup>-1</sup>(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  $\sim 27200 \,\text{GgCyr}^{-1}$ taken up by UK forests. However, even if roughly half of NEP<sub>av</sub> 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 kgC 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<sub>av</sub> response of Magnani *et al.* was only in relation to wet 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<sub>av</sub>. 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<sub>av</sub> to affect the reported C:N response. We combine our estimates of total N deposition with the NEP<sub>av</sub> data of Magnani *et al.* and other climato-logical parameters to investigate possible interactions.

Having accounted for total N deposition, we find the evidence of a substantial remaining climatological effect on NEP<sub>av</sub>, 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 multisite 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<sub>dep</sub> remains an important driver of NEP<sub>av</sub>, the dataset of Magnani *et al.* (2007) does not support their conclusion that NEP<sub>av</sub> is 'overwhelmingly driven by nitrogen deposition.'

# Methods

In the first stage we sought to relate the Magnani *et al.* (2007) NEP $_{\rm av}$  values to independent estimates of wet and dry N<sub>dep</sub>. Although their dataset included sites from around the globe, the observed response between NEP<sub>av</sub> and N<sub>dep</sub> 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<sub>dep</sub> 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<sub>dep</sub> 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 Although not perfect, analysis. 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<sub>dep</sub> 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 NEGTAP (National Expert Group on Transboundary Air Pollution) model to estimate wet and dry N<sub>dep</sub> for the four surrounding 5 km grid squares. The NEGTAP 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; NEGTAP, 2001; Sutton *et al.,* 2001).

It is worth noting that Magnani et al. (2007) focused their analysis of climatological interactions with NEP<sub>av</sub> 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<sub>av</sub> 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  $0.5^{\circ}$  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 Ndep at the sites, we compared the NEP<sub>av</sub> 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<sub>av</sub> vs. total N<sub>dep</sub>, 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<sub>av</sub>) of midlatitude forests and different estimates of atmospheric nitrogen deposition (N<sub>dep</sub>). Measured NEP<sub>av</sub> vs. wet deposition estimates of Magnani *et al.* (2007) ( $\bigcirc$ , C:N = 726:1) are compared with EMEP model estimates of wet deposition ( $\triangle$ , C:N = 428:1) and total N deposition ( $\bigcirc$ , C:N = 177:1) for 2000, and with NEGTAP high-resolution wet ( $\times$ ) and total (+) N<sub>dep</sub> 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<sub>dep</sub> estimates were less than  $2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (their Fig. 3d). Overall, using the EMEP wet N<sub>dep</sub> 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<sub>av</sub> 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<sub>dep</sub> 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<sub>dep</sub>, the implied NEP<sub>av</sub> 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<sub>dep</sub>, and how this uncertainty propagates to estimates of the NEPav response to N<sub>dep</sub>. However, while recognizing these uncertainties, the comparisons show that it is essential to quantify both wet and dry N<sub>dep</sub> in order to derive sound values of the NEP<sub>av</sub> 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<sub>dep</sub>, 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<sub>av</sub>: total N<sub>dep</sub> response. A key point of interest is that Magnani et al. (2007) demonstrated a major temperature sensitivity in both GPPav and REav. As NEPav is simply the difference between these terms, there is no a priori reason why there should be no NEP<sub>av</sub> response to temperature. In fact, although the correlation between NEP<sub>av</sub> and mean annual temperature reported by Magnani et al.  $(R^2 = 0.41)$  is weaker than that with wet N<sub>dep</sub>  $(R^2 = 0.98)$ , the relationship between NEP<sub>av</sub> and temperature remains substantial (accounting for a change of  $3 \text{ Mg C} \text{ ha}^{-1} \text{ yr}^{-1}$  across the full range of their sites). It is therefore possible that thermal differences between sites explain part of the apparent NEP<sub>av</sub> response to total  $N_{dep}$ . If the temperature response (Fig. 3c of Magnani *et al.*, 2007) is used to normalize the values of NEP<sub>av</sub> 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<sub>av</sub>. Figure 2 shows the NEP<sub>av</sub> 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 Brav/Bilos, southwest France; Site 19, Roccarespampani, Italy). These two sites are shown as clear outliers in an otherwise close relationship between NEPav and GDD5 (Fig. 2b). Excluding these two sites, the relationship gives  $R^2 = 0.98$ , which is even higher than the relationship between NEP<sub>av</sub> and total N<sub>dep</sub>. As a consequence, multiple regression of total Ndep and GDD5 vs. NEP<sub>av</sub> for the remaining sites ( $R^2 = 0.99$ , P = 0.012), assigns the variation first to GDD5. This reduces the estimated NEP<sub>av</sub> response to N<sub>dep</sub> (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<sub>dep</sub> 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<sub>av</sub> of Magnani *et al.* (2007) and two climatological variables estimated at  $0.5^{\circ}$ : (a) actual evapotranspiration/potential evapotranspiration (AET/PET), (b) growing degree days above 5 °C (GGD5). The two outlier sites are Site 10 (Le Bray/Bilos, SW France) and Site 19 (Roccarespampani, Italy) according to the site numbering of Magnani *et al.* 

#### Ecosystem modeling

Having corrected the Magnani et al. (2007) NEPav response for total N<sub>dep</sub> 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<sub>av</sub> to total N<sub>dep</sub> fits within the range of the model estimates. Superficially, this might appear to show that the NEP<sub>av</sub> dataset of Magnani *et al.* (2007) combined with EMEP total N<sub>dep</sub> for 2000 is broadly consistent with the existing models. However, a closer assessment shows that the NEP<sub>av</sub> 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 (5.8–25.7 kg N ha<sup>-1</sup> yr<sup>-1</sup>, 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<sub>dep</sub>.

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<sub>av</sub>) response to total N<sub>dep</sub> (EMEP for 2000, ●) with the NEP<sub>av</sub> responses to N<sub>dep</sub> 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<sub>av</sub> estimates vs. total N<sub>dep</sub> (---, 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<sub>tree</sub>/ dN<sub>tree</sub>) 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<sub>av</sub> for the stand lifetimes of the 22 forests, we related the EFM results to the modeled total N<sub>dep</sub> 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<sub>av</sub> response to total N<sub>dep</sub> (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 NEPav (Magnani et al., 2007) vs. total Ndep (EMEP for 2000). Using the model, however, we see that the high NEP<sub>av</sub> response is an artefact of the single-factor regression. Multiple regression of the EFM NEP<sub>av</sub> shows that both temperature and precipitation are significant factors (P = 0.003and 0.02, respectively). Accounting for these reduces the C:N response to 54:1 (P = 0.17), with the multifactor 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  $dC_{tree}/dN_{tree}$ 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<sub>av</sub>. 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<sub>dep</sub> remains an important determinant of NEP<sub>av</sub>, as illustrated by the model responses in Fig. 3, it cannot be concluded that N<sub>dep</sub> is the 'overwhelming driver' of NEP<sub>av</sub>.

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<sub>av</sub> with GDD5 and AET/PET), and the uncertainties in total  $N_{dep'}$  we arrive at an NEP<sub>av</sub> 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.

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