

floors "in all cases". Atmospheric nitrogen deposition is actually intercepted by the forest canopy, particularly at the nine closed-canopy forests studied.

It is known that forest canopies chemically interact with HNO_3 , NO_x and NH_3 gases (among others), as well as with the NO_3^- and NH_4^+ ions in particulate matter. The Integrated Forest Study⁴, covering 13 sites with a wide range of North American and European forest types and atmospheric nitrogen deposition, varying from 5 to 30 kg per hectare per year, reported that "an average 40% of the incoming inorganic N is retained in or transformed at passage through the canopy; the net canopy exchange is greatest at those sites receiving the highest atmospheric N input." At some sites in this study in the eastern United States, the canopy retention of atmospheric inorganic nitrogen deposition is very high: for example, at Howland Forest, Maine⁵, nitrate canopy retention is about 90% and ammonium canopy retention is more than 80%. Retained nitrogen deposition can also be rapidly assimilated by canopy foliage⁶.

The ^{15}N applied by Nadelhoffer *et al.*¹ to the forest floor would have bypassed the canopy retention and assimilation pathway. The nitrogen deposition allocated to the non-woody and woody biomass ecosystem pools (15 and 5%, respectively; Table 2 of ref. 1) may have been significantly increased if it had been possible to apply the labelled nitrogen to the forest canopy.

Doubling or tripling the percentage of nitrogen deposition allocated to woody biomass (10 or 15%, rather than the 5% used) would increase forest carbon uptake by 50–100% over that estimated by Nadelhoffer *et al.* The woody-biomass nitrogen allocation may be increased several-fold, and could be determined by using labelled nitrogen applied to the forest canopy.

Using a figure of 5.1×10^{12} g per year as the global nitrogen deposition to forests may also lead to an underestimate. It is recognized that there is much uncertainty in the estimates of forest nitrogen deposition^{2,3}, particularly in the case of $\text{NH}_x\text{-N}$ deposition, which may be substantially greater^{7,8} than the 2×10^{12} g nitrogen per year considered in ref. 1. Total anthropogenic nitrogen deposition has been estimated to be as much as 18×10^{12} g per year to temperate and boreal forests⁹, which is three or more times the value reported in ref. 1. These two points can provide an upper bound for estimates of forest carbon sequestration of $1\text{--}2 \times 10^{15}$ g carbon per year, with the range dependent on the still poorly known nitrogen deposition allocated to woody biomass.

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Nadelhoffer *et al.* reply — Jenkinson *et al.* and Sievering are justifiably concerned that our ^{15}N additions to forest floors do not account for the potential uptake of nitrogen input by forest canopies. We agree that canopies can remove nitrogen from the atmosphere, resulting in inputs to forest floors that are less than the total nitrogen deposition. A North American study¹ has suggested that canopies remove, on average, 16% of total (organic + inorganic) atmospheric nitrogen input to forests, and concluded that nitrogen uptake by the canopy is probably small relative to the nitrogen requirements of trees. Spraying ^{15}N -labelled ammonium and nitrate on the crowns of five-year-old Norway spruce indicated that foliar uptake in mature forests probably constitutes only a small percentage of annual nitrogen uptake².

Although canopies can remove nitrogen from bulk deposition, the extent to which this nitrogen is biologically available and stimulates wood growth is poorly understood. Throughfall nitrogen fluxes at our sites either exceed the measured bulk nitrogen deposition or closely agree with modelled total deposition^{3–5}, so their use as a proxy for nitrogen deposition is reasonable and does not compromise our conclusions.

We think it is unlikely that "pool substitution" of unlabelled inorganic nitrogen for ^{15}N tracers in soils biased our estimates of throughfall uptake by trees, as claimed by Jenkinson *et al.*, who found this mechanism operating in theoretical models⁶ and in potted, but not in field-grown, plants⁷. Comparison of the amounts of our tracer additions to the amount of unlabelled inorganic nitrogen already present in our soils with those amounts in their theoretical analysis (see Fig. 1 of ref. 6) indicates that pool substitution is unimportant at the low ^{15}N enrichment used in our throughfall manipulations.

We agree that forest soils can serve as long-term carbon sinks and that carbon turnover times in soil pools are longer than in trees. Nevertheless, as nearly all carbon enters forests through trees, it is here that the influence of nitrogen inputs on carbon uptake is important. We point out, however, that our simple stoichiometric budget

(Table 2 of ref. 8) actually factors in the role of soils, with soil storage calculated as the product of the C:N ratio and nitrogen immobilization in soils.

Finally, we recognize that there is a wide range of estimates for nitrogen deposition on temperate forests. This is because of uncertainties and likely but unknown biases in the atmospheric mixing models, emissions data and site-specific wet + dry nitrogen deposition data used to generate spatial predictions of nitrogen deposition on forests. Our temperate-forest deposition value of 5.1×10^{12} g nitrogen was derived from a comparison of modelled NO_y and NH_x deposition estimates⁹. If this value were to be in serious disagreement with estimates based on greatly improved monitoring and modelling efforts, then our assessment of the effects of nitrogen deposition on temperate-forest carbon uptake would need to be revised.

Future estimates of this effect must also consider spatially explicit patterns of nitrogen loss from forests in relation to nitrogen deposition and land use¹⁰, the likelihood of narrowing C:N ratios under increased nitrogen input, and possible nutritional imbalance of tree tissue subjected to high nitrogen input. Meanwhile, our tracer experiments indicate that, although nitrogen deposition in forests accounts for some of the northern-temperate CO_2 sink, other factors must account for most of this sink.

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