

Increased tree carbon storage in response to nitrogen deposition in the US

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Human activities have greatly accelerated emissions of both carbon dioxide and biologically reactive nitrogen to the atmosphere^{1,2}. As nitrogen availability often limits forest productivity³, it has long been expected that anthropogenic nitrogen deposition could stimulate carbon sequestration in forests⁴. However, spatially extensive evidence for deposition-induced stimulation of forest growth has been lacking, and quantitative estimates from models and plot-level studies are controversial^{5–10}. Here, we use forest inventory data to examine the impact of nitrogen deposition on tree growth, survival and carbon storage across the northeastern and north-central USA during the 1980s and 1990s. We show a range of growth and mortality responses to nitrogen deposition among the region's 24 most common tree species. Nitrogen deposition (which ranged from 3 to 11 kg ha⁻¹ yr⁻¹) enhanced the growth of 11 species and decreased the growth of 3 species. Nitrogen deposition enhanced growth of all tree species with arbuscular mycorrhizal fungi associations. In the absence of disturbances that reduced carbon stocks by more than 50%, above-ground biomass increment increased by 61 kg of carbon per kg of nitrogen deposited, amounting to a 40% enhancement over pre-industrial conditions. Extrapolating to the globe, we estimate that nitrogen deposition could increase tree carbon storage by 0.31 Pg carbon yr⁻¹.

During the 1990s, terrestrial ecosystems in the Northern Hemisphere absorbed approximately 1.7 Pg carbon (C) yr⁻¹, or ~25% of the emissions from fossil fuel combustion (6.4 Pg C yr⁻¹; ref. 1). The causes of this sink have not been quantitatively partitioned, but proposed mechanisms include forest regrowth and forest growth enhancement from climate change, CO₂ fertilization, changes in forest management and nitrogen (N) deposition^{1,10}. Identifying the mechanisms that control this C sink is critical for managing and predicting its future behaviour. Estimates of the magnitude of N deposition effects on global forest C balance vary greatly, with recent controversy^{5–9} particularly focused on the plausibility of a large N-induced C sink reported for 20 (mostly European) chronosequences (>200 kg C for each kilogram of N deposited; refs 6, 7).

Global biogeochemical models estimate that forest C sinks from N deposition range from 0.24 to 2.0 Pg C yr⁻¹ (refs 11–13). In contrast, an analysis of forest inventory data from five US states discerned little growth enhancement resulting from any environmental change over the past century¹⁴. Plot-level ¹⁵N tracer experiments show that most added N is retained in soil rather than trees, leading to estimates of a small N-induced forest C sink (0.14 Pg C yr⁻¹ in trees; 0.25 Pg C yr⁻¹ in trees + soil; ref. 15). Long-term fertilization studies show that N additions can provide modest growth enhancements¹⁶ but that N saturation can induce mortality, which decreases C storage in live biomass^{17,18}, casting

some doubt on both the magnitude and the direction, of future forest C responses. Spatial covariation between N deposition and patterns of tropospheric ozone and sulphur pollution may further offset N-induced growth enhancement¹⁹. Here, we use spatially extensive forest inventory data to discern the effect of N deposition on the growth and survival of the 24 most common tree species of the northeastern and north-central US, as well as the effect of N deposition on C sequestration in trees across the breadth of the northeastern US.

Species-level responses to N deposition are critical to projections of how tree communities will change as a result of a range of factors, including succession, climate change and host-specific pests²⁰. Individual tree growth responded to N deposition for 14 of the 24 species examined; however, the direction, shape and magnitude of the response varied by species (Fig. 1, Table 1). Three of the four most abundant species (*Acer rubrum*, *A. saccharum* and *Quercus rubra*) showed strong positive growth responses (>4% increase in C increment per kg N ha⁻¹ yr⁻¹). The largest growth enhancements (16–18% per kg N ha⁻¹ yr⁻¹) occurred in *Liriodendron tulipifera* and *Prunus serotina*, two valuable timber species. Mycorrhizal association may also influence the response to N deposition, as all five of the tree species with arbuscular mycorrhizal associations responded positively (*Acer rubrum*, *A. saccharum*, *Fraxinus americana*, *Liriodendron tulipifera*, and *Prunus serotina*). Unlike ectomycorrhizal fungi, arbuscular mycorrhizal fungi are unable to produce enzymes that break down soil organic N (ref. 21), thus trees with arbuscular associations may be more likely to benefit from increased availability of soil inorganic N associated with N deposition.

All three of the species with net negative growth responses were evergreen conifers (*Pinus resinosa*, *Picea rubens*, *Thuja occidentalis*). The species with the largest decline in growth (9% decrease per kg N ha⁻¹ yr⁻¹) was *Pinus resinosa*, a species shown to respond negatively to chronic N fertilization in a long-term N-addition experiment in central Massachusetts¹⁷. The decline in growth observed here could be due to a range of factors, including N-induced leaching of soil base cations²², increased vulnerability to secondary stressors (drought, insects) or suppression by more competitive species²³.

The net effect of N deposition on tree C stocks depends on not only the growth responses but also the mortality response. N deposition influenced the survivorship of 11 of the 23 species examined (Fig. 1 and Table 1); three species showed increased survivorship and eight showed decreased survivorship across the range of N deposition. All eight of the species showing decreased survivorship had ectomycorrhizal associations (Table 1), further suggesting that mycorrhizal association influences tree species response to N deposition. The growth and lifespan of two tree species with arbuscular mycorrhizal associations—*Prunus serotina*

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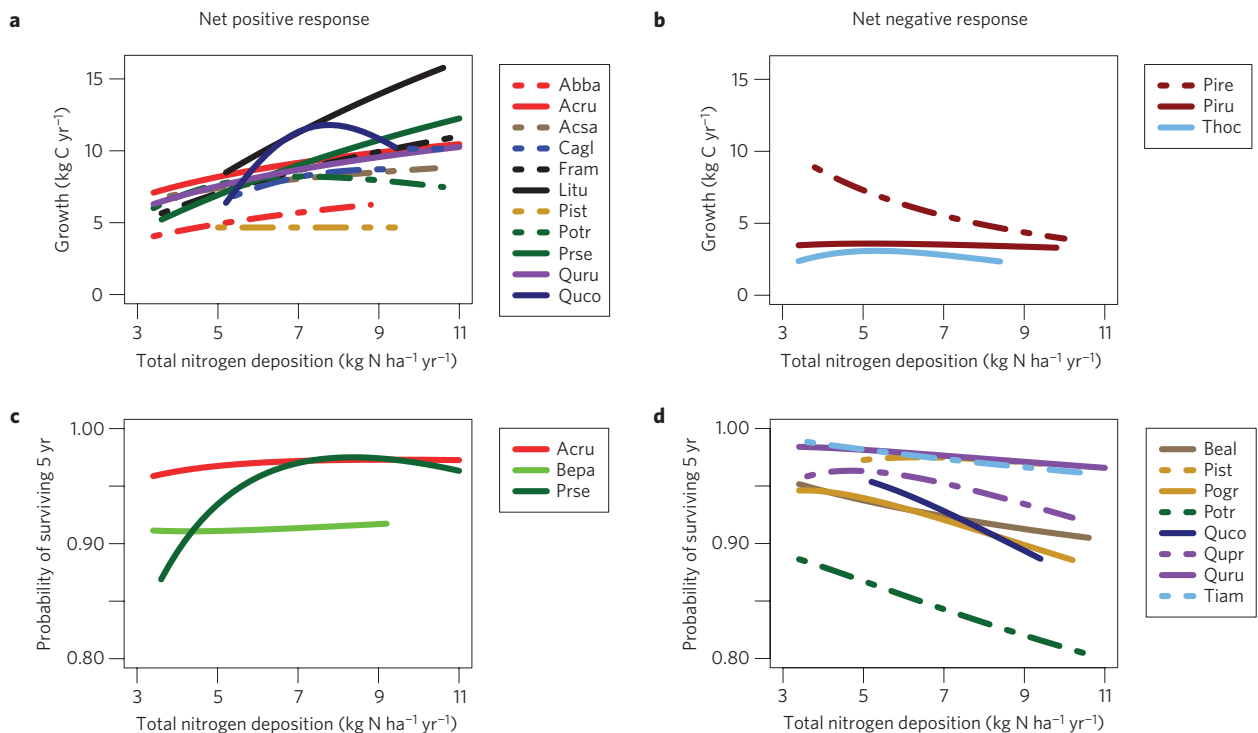


Figure 1 | Growth and survival response to increasing nitrogen deposition. **a–d**, The annual above-ground carbon increment (**a–b**) and five-year survival rate (**c–d**) as a function of total (wet + dry) inorganic N deposition for individual trees of the 24 most common species in a 19-state region of the US. Species that did not respond to nitrogen deposition are not shown. See Table 1 for the species abbreviation codes and Supplementary Fig. S1 for the survival response of *Abies balsamea*.

and *Acer rubrum*—increased with N deposition; *P. serotina* showed especially large changes in both. No species showed reduction in both growth and survivorship.

At the stand level, the growth by all trees that survived the remeasurement period increased across the observed range of N deposition (3–11 kg C ha⁻¹ yr⁻¹; Fig. 2a and Table 2). The fertilization effects of N on tree growth presumably drove this relationship. Considering both growth and mortality responses while excluding major disturbance (that is, excluding plots that lost more than 50% of the C stock over the measurement period), annual net above-ground C increment increased nearly linearly (5.5% increase per kg N ha⁻¹ yr⁻¹) over the observed range of N deposition (Fig. 2b and Table 2). This response is steeper (5.5% versus 1.5%) than observed for two conifer species in 363 European plots spanning a larger range of N deposition²⁴, perhaps owing to a greater responsiveness at the lower N deposition values observed in this study. However, the relationship between net C increment and N deposition is not present if all levels of disturbance are considered, as the variability induced by large stochastic mortality events obscured the effects of N on growth (Fig. 2a). As the response was nearly linear, there was no evidence for N saturation at the stand level at the rates of N deposition observed in this data set, although it may occur at higher rates of N deposition²². At the species level, some species showed decreased growth or decreased survivorship at the higher levels of N deposition, suggesting that these species may be more sensitive than others to the deleterious effects of N inputs, as well as other pollutants that co-vary with N deposition (Fig. 1). N deposition explained a small amount of variation in growth, survivorship and C gain across the region, indicating that many factors affect forest C balance. Nonetheless, the statistical analyses provide strong support for a N effect on regional forest C gain in addition to the effect of climate alone (Table 2).

Averaged across all plots in the 13-state subset of our study area, anthropogenic N deposition, in the absence of major disturbance,

enhanced above-ground C increment in trees by 40% (37–47%; two-unit support interval, approximately a 95% confidence interval in a likelihood framework) over preindustrial conditions (calculated using a linear extrapolation to an assumed preindustrial inorganic N deposition of approximately 1 kg ha⁻¹ yr⁻¹ (ref. 2)). This response is integrative in that it includes the direct effects of N deposition on tree growth through soil fertilization, foliar N uptake and other potential interactions between N deposition and other environmental changes, including CO₂ fertilization. It greatly exceeds the <2% growth enhancement deduced from biomass and age information from similar inventory data from fewer states¹⁰, although others have highlighted uncertainties in that previous analysis²⁵. It also exceeds the 23% enhancement of net primary production anticipated for the year 2050 from a doubling of atmospheric CO₂ over preindustrial levels, as estimated using free-air CO₂ enrichment studies²⁶.

This enhancement of above-ground C storage (Fig. 2b) averaged 61 kg C ha⁻¹ yr⁻¹ per kg increase in N deposition (51–82 kg C ha⁻¹ yr⁻¹ per kg; two unit support interval). This C/N response ratio does not include infrequently measured forms of N deposition, such as NH₃, NO and NO₂ gases, or organic N, nor does it include the effects of N deposition on root biomass or soil C stocks, which may have important influences on the the sink^{5,10}. Although variable, below-ground tree biomass often represents roughly 20% of above-ground biomass²⁷. Therefore, the corresponding enhancement of total tree C would be 73:1 (61–98:1) kg C ha⁻¹ yr⁻¹ per kg ha⁻¹ yr⁻¹. This ratio of C sequestration per unit N deposition in tree C stocks exceeds ratios estimated from European forest inventory data (20–40:1; above-ground C in trees; ref. 8), partitioning inferred from plot-level ¹⁵N tracer studies (25:1; C in trees; ref. 15) and plot-level fertilization studies in Scandinavia (–1 to 53:1; ref. 16). The ratio is substantially lower than the whole-ecosystem (net ecosystem production) estimate of 200:1 derived from plot-level

Table 1 | Species included in the analysis of individual growth and survival, with common names, sample size, ecological attributes and results of AIC analysis.

Species	Abbreviation	Common name	Sample size*	% abundance	Ecological attributes	Growth					Survival			
						Size and climate	Size, climate, and N deposition	R ²	Mean predicted growth rate (kg Cyr ⁻¹)	% growth change per kg N ha ⁻¹ yr ⁻¹ †	Size and climate	Size, climate and N deposition	Mean predicted five-year survival rate	% five-year survival rate change per kg N ha ⁻¹ yr ⁻¹ †
<i>Abies balsamea</i>	Abba	Balsam fir	5,650	3.3	EM, EC	6.79	0	0.22	10.15	12.3	144.4	0	0.52	0.06
<i>Acer rubrum</i>	Acru	Red maple	23,047	13.6	AM, DH	277.29	0	0.49	18.39	6.3	8.33	0	0.97	0.19
<i>Acer saccharum</i>	Acsa	Sugar maple	18,480	10.9	AM, DH	65.47	0	0.35	16.04	4.2	0	1.81	0.98	
<i>Betula alleghaniensis</i>	Beal	Yellow birch	3,889	2.3	EM, DH	0	16.53	0.25	10.29		5.97	0	0.93	-0.68
<i>Betula lenta</i>	Bele	Black birch	2,895	1.7	EM, DH	0	58.56	0.47	14.58		0	0.94	0.97	
<i>Betula papyrifera</i>	Bepa	Paper birch	4,393	2.6	EM, DH	0	0.61	0.26	7.42		12.92	0	0.91	0.11
<i>Carya glabra</i>	Caga	Pignut hickory	2,554	1.5	EM, DH	11.51	0	0.55	16.69	7.2	0	2.87	0.97	
<i>Fagus grandifolia</i>	Fagr	American beech	6,697	3.9	EM, DH	0	199.49	0.59	15.02		0	19.28	0.97	
<i>Fraxinus americana</i>	Fram	White ash	6,538	3.9	AM, DH	16.03	0	0.5	18.15	13.0	0	1.7	0.96	
<i>Liriodendron tulipifera</i>	Litu	Tulip poplar	6,179	3.6	AM, DH	130.16	0	0.56	29.79	16.0	0	4.26	0.98	
<i>Pinus resinosa</i>	Pire	Red pine	3,333	2.0	EM, EC	62.55	0	0.31	10.82	-9.0	0	3.16	0.99	
<i>Picea rubens</i>	Piru	Red spruce	2,930	1.7	EM, EC	26.66	0	0.26	7.18	-0.1	0	11.38	0.92	
<i>Pinus strobus</i>	Pist	White pine	8,272	4.9	EM, EC	0.44	0	0.32	11.69	0.9	21.68	0	0.97	-0.08
<i>Populus grandidentata</i>	Pogr	Quaking aspen	3,233	1.9	EM, DH	0	32.78	0.34	14.50		6.7	0	0.92	-0.94
<i>Populus tremuloides</i>	Potr	Trembling aspen	5,462	3.2	EM, DH	31.48	0	0.39	16.30	3.4	17.21	0	0.85	-1.30
<i>Prunus serotina</i>	Prse	Black cherry	6,585	3.9	AM, DH	41.41	0	0.54	24.41	18.0	10.82	0	0.97	1.47
<i>Quercus alba</i>	Qual	White oak	12,130	7.1	EM, DH	0	127.03	0.66	15.23		0	0.73	0.98	
<i>Quercus coccinea</i>	Quco	Scarlet oak	2,406	1.4	EM, DH	157.61	0	0.63	22.81	14.4	14.66	0	0.93	-1.67
<i>Quercus prinus</i>	Qupr	Chestnut oak	8,318	4.9	EM, DH	0	192.24	0.62	16.06		4.82	0	0.95	-0.57
<i>Quercus rubra</i>	Quru	Red oak	11,861	7.0	EM, DH	137.79	0	0.66	22.16	8.3	3.17	0	0.98	-0.24
<i>Quercus velutina</i>	Quve	Black oak	7,328	4.3	EM, DH	0	237.11	0.61	23.86		0	3.16	0.95	
<i>Thuja occidentalis</i>	Thoc	White cedar	6,512	3.8	EM, EC	43.25	0	0.31	6.08	-0.01	0	2.95	0.94	
<i>Tilia americana</i>	Tiam	Basswood	3,450	2.0	EM, DH	0	3.27	0.48	14.51		0.04	0	0.97	-0.39
<i>Tsuga canadensis</i>	Tsca	Eastern hemlock	7,676	4.5	EM, EC	0	5.59	0.47	11.38		0	1.47	0.98	

The ecological attributes include mycorrhizal association (arbuscular (AM) versus ecto (EM) mycorrhizal) and plant functional type (deciduous hardwood (DH) versus evergreen conifer (EC)). The model comparison from likelihood analysis of individual tree annual above-ground carbon increment (growth) and five-year survival rate for the 24 most common tree species is shown along with the % response per kg ha⁻¹ yr⁻¹ of extra N deposition. Species acronyms are given for reference to the legends of the figures. ΔAIC is the difference between the AIC of the best model (ΔAIC = 0) and alternative models; a larger AIC indicates a poorer model fit. Goodness of fit (R²) is reported for the best model. The climate effect included the most parsimonious model of annual mean temperature and precipitation, either one alone, or neither, as indicated by differences in AIC.

* Number of stems used in the analysis of survival (that is, alive at the time of the first census and not harvested or missing at the time of the second census).

† Assumes a linear response between the minimum and maximum nitrogen deposition observed for that species.

eddy flux tower and chronosequence data^{6,7}; a 127 kg C per kg of N response in soils or dead wood would be needed to make up the difference between our tree response and the 200:1 net ecosystem production response. Although the soil response is highly uncertain, a recent review of Scandinavian N fertilization studies demonstrated soil responses that ranged from 1 to 20:1 kg C per kg of N (ref. 16).

Globally, we estimate that N deposition could account for a 0.31(0.26–0.42) Pg C yr⁻¹ sink into above-ground trees. This estimate of the global sink was calculated by multiplying the C/N response measured in this study (61:1) by a conservative estimate of total N deposition to forests (5.1 Tg N yr⁻¹; ref. 11), predominately in temperate regions. Similar stoichiometric-based approaches have

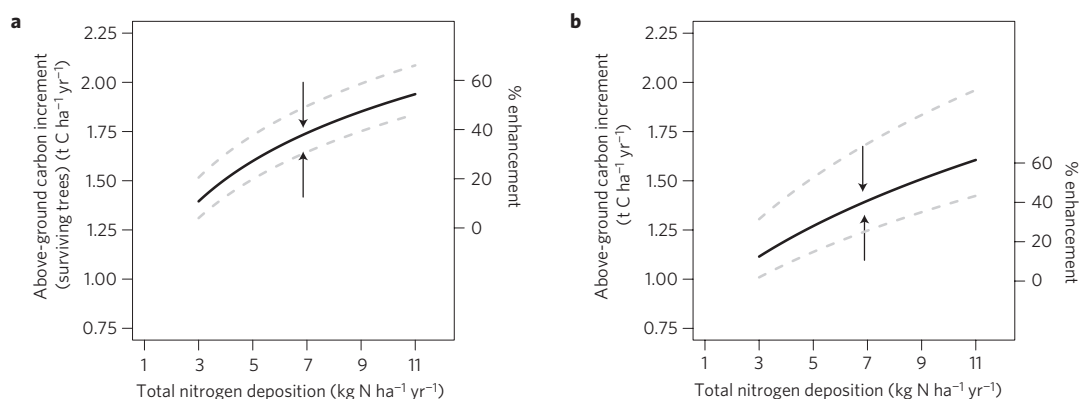


Figure 2 | Annual above-ground carbon increment increases with nitrogen deposition. **a,b**, The relationship between total (wet + dry) inorganic N deposition and annual above-ground growth of surviving trees (**a**) and net annual above-ground carbon increment (excluding plots with >50% loss of carbon stocks) (**b**) at the plot level. The per cent enhancement uses preindustrial N deposition ($1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) as a baseline and a linear extrapolation of the response. The mean annual N deposition ($6.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) estimated for the forest inventory data is shown with the arrows. Two-unit support intervals are plotted as grey-dashed lines.

Table 2 | ΔAIC , goodness of fit (R^2) and C/N response ratio from the likelihood analysis of plot-level annual above-ground carbon increment and annual above-ground carbon increment of the trees that survived the measurement period.

Plot-level response variable	Disturbance exclusion	Sample size	ΔAIC		NP	R^2	C/N response ratio
			Size, temperature, precipitation	Size, temperature, precipitation and nitrogen			
Surviving tree growth	None	4,817	32.83	0	9	0.47	68:1
Net annual above-ground carbon increment	>50% net biomass lost	4,686	4.15	0	9	0.08	61:1
Net annual above-ground carbon increment	None	4,817	2.75	0	9	0.06	0

ΔAIC is the difference between the AIC of the best model ($\Delta\text{AIC} = 0$) and alternative models. R^2 is reported for the best model. NP is the number of parameters in the best model (including any parameters estimated for the error term).

been used by others to obtain global estimates of the forest C sink attributed to N deposition^{15,28}. Although there is uncertainty in applying a single C/N response to all temperate forests, such exercises illustrate the global-scale implications of reported growth enhancements. Our estimate of a N-induced global C sink is greater than that estimated using plot-level ¹⁵N tracers ($0.14 \text{ Pg C yr}^{-1}$ in trees¹⁵) and a recent global biogeochemical model ($0.24 \text{ Pg C yr}^{-1}$ in trees and soils¹³). In contrast, our global C sink estimate is substantially lower than the sinks in trees and soil predicted by earlier global biogeochemical models ($1.5\text{--}2.0 \text{ Pg C yr}^{-1}$ (ref. 11)) or inferable from the 200:1 C/N response reported for 20 intensive C monitoring sites ($1.02 \text{ Pg C yr}^{-1}$ (ref. 7)). The latter estimates imply that most of the terrestrial C sink (1.7 Pg C yr^{-1} (ref. 1)) can be attributed to N deposition, despite evidence that land-use history has an important role²⁹.

Thus, we show that N deposition is an important mechanism contributing to C sequestration within these temperate forests, but is unlikely to explain all of the observed terrestrial C sink. Furthermore, forest response to N deposition depends on the species present, and N deposition will probably influence future forest demography by altering tree growth and survival.

Methods overview

National forest inventories measure the growth and survival of individual trees, and provide an invaluable opportunity for assessing patterns of regional C balance. Here, we used forest inventory data for the 24 most common tree species occurring on 20,067 plots remeasured during the early 1980s to mid-1990s by the US Forest Service Forest Inventory and Analysis (FIA) Program. The plots span a 19-state region bounded by Maine in the northeastern USA, to Virginia

and Kentucky, and to longitude 90° west in the states of Wisconsin and Illinois. We used a model-selection approach to ask whether data on mean annual N deposition (wet NO_3^- and NH_4^+ and dry HNO_3 gas and particulate NH_4 and NO_3) improved models that predicted stand-level C increment and species-specific growth and survivorship as a function of both climate (mean annual temperature and precipitation) and C stocks at the beginning of the measurement period. The stand-level analysis was carried out using all species on a 13-state subset of the region that used fixed-radius plot designs ($n = 4,817$ plots); the six states (Indiana, Illinois, Kentucky, Michigan, Virginia and Wisconsin) with variable-radius plots were excluded. The stand-level analysis also excluded plots with trees harvested between measurement periods.

We compiled a data set on tree growth in carbon, tree survival, plot-level net C increment and plot-level C increment of living trees during the 1970s–1990s across the northeastern and north-central US. For each plot, the mean annual temperature, mean annual precipitation and mean annual total (wet + dry) inorganic (nitrate and ammonium) nitrogen deposition for each plot were estimated using the geographic location of the plot and spatially resolved data on temperature, precipitation and N deposition (see Supplementary Information for more details). For each of the independent variables (tree-level growth, tree-level survival, plot-level net C increment and plot-level C increment of living trees), we solved for the maximum likelihood estimates for model parameters in models that included the influence of climate and tree size (or plot C stock) on the variable. The climate effect included mean annual temperature, mean annual precipitation, or both, depending on which had the lowest Akaike Information Criterion³⁰ (AIC) and was therefore the most parsimonious (that is, the best model fit for the fewest parameters). To determine whether N deposition influenced the independent variables beyond that of size and climate, we added a lognormal nitrogen deposition term to the model that included size and climate, estimated the parameters using maximum likelihood and compared the AIC between the models with and without N. If the model that included N deposition had the lowest AIC, we used the model parameters to assess the response of the variable to N deposition. Supplementary Information provides further details on the data sources, data compilation and models used in the analyses.

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References

- Denman, K. L. *et al.* in *IPCC Climate Change 2007: The Physical Science Basis* (eds Solomon, S. *et al.*) (Cambridge Univ. Press, 2007).
- Galloway, J. N. *et al.* Nitrogen cycles: Past, present, and future. *Biogeochemistry* **70**, 153–226 (2004).
- LeBauer, D. S. & Treseder, K. K. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**, 371–379 (2008).
- Melillo, J. M. & Gosz, J. R. in *The Major Biogeochemical Cycles and Their Interactions* (eds Bolin, B. & Cook, R. B.) 177–222 (John Wiley & Sons, 1983).
- Janssens, I. A. & Luyssaert, S. Nitrogen's carbon bonus. *Nature Geosci.* **2**, 318–319 (2009).
- Magnani, F. *et al.* The human footprint in the carbon cycle of temperate and boreal forests. *Nature* **447**, 849–851 (2007).
- Magnani, F. *et al.* Ecologically implausible carbon response? Reply. *Nature* **451**, E3–E4 (2008).
- De Vries, W. *et al.* Ecologically implausible carbon response? *Nature* **451**, E1–E3 (2008).
- Sutton, M. *et al.* Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Glob. Change Biol.* **14**, 2057–2063 (2008).
- Reay, D. S. *et al.* Global nitrogen deposition and carbon sinks. *Nature Geosci.* **1**, 430–437 (2008).
- Holland, E. A. *et al.* Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *J. Geophys. Res.* **102**, 15849–15866 (1997).
- Townsend, A. R., Braswell, B. H., Holland, E. A. & Penner, J. E. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. *Ecol. Appl.* **6**, 806–814 (1996).
- Thornton, P. E., Lamarque, J., Rosenbloom, N. A. & Mahowald, N. M. Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability. *Glob. Biogeochem. Cycles* **21**, GB4018 (2007).
- Caspersen, J. P. *et al.* Contributions of land-use history to carbon accumulation in US forests. *Science* **290**, 1148–1151 (2000).
- Nadelhoffer, K. J. *et al.* Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* **398**, 145–148 (1999).
- Hyvönen, R. *et al.* Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry* **89**, 121–137 (2008).
- Magill, A. H. *et al.* Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecol. Management* **196**, 7–28 (2004).
- Wallace, Z., Lovett, G., Hart, J. & Machona, B. Effects of nitrogen saturation on tree growth and death in a mixed-oak forest. *Forest Ecol. Manage.* **243**, 210–218 (2007).
- Ollinger, S. V., Aber, J. D., Reich, P. B. & Freuder, R. J. Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO₂ and land use history on the carbon dynamics of northern hardwood forests. *Glob. Change Biol.* **8**, 545–562 (2002).
- Lovett, G. M. *et al.* Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* **56**, 395–405 (2006).
- Chalot, M. & Brun, A. Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *Fems Microbiol. Rev.* **22**, 21–44 (1998).
- Aber, J. *et al.* Nitrogen saturation in temperate forest ecosystems—hypotheses revisited. *Bioscience* **48**, 921–934 (1998).
- Hautier, Y., Niklaus, P. A. & Hector, A. Competition for light causes plant biodiversity loss after eutrophication. *Science* **324**, 636–638 (2009).
- Solberg, S. *et al.* Analyses of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: A stand growth approach. *Forest Ecol. Manage.* **258**, 1735–1750 (2009).
- Joos, F., Prentice, I. C. & House, J. I. Growth enhancement due to global atmospheric change as predicted by terrestrial ecosystem models: Consistent with US forest inventory data. *Glob. Change Biol.* **8**, 299–303 (2002).
- Norby, R. J. *et al.* Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proc. Natl Acad. Sci. USA* **102**, 18052–18056 (2005).
- Jenkins, J. C., Chojnacky, D. C., Heath, L. S. & Birdsey, R. A. National-scale biomass estimators for United States tree species. *Forest Sci.* **49**, 12–35 (2003).
- Schindler, D. W. & Bayley, S. E. The biosphere as an increasing sink for atmospheric carbon—estimates from increased nitrogen deposition. *Glob. Biogeochem. Cycles* **7**, 717–733 (1993).
- Hurt, G. C. *et al.* Projecting the future of the US carbon sink. *Proc. Natl Acad. Sci. USA* **99**, 1389–1394 (2002).
- Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* 2nd edn (Springer, 2002).

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Author contributions

R.Q.T., C.D.C., K.C.W. and C.L.G. all contributed to the development of project ideas, design, analysis interpretation and to writing of the manuscript, with C.L.G. and R.Q.T. originating the project. In addition, C.D.C. and R.Q.T. assembled the FIA and climate data and carried out the statistical analyses, K.C.W. developed the N deposition estimates and C.L.G. and R.Q.T. provided the carbon framework.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions>. Correspondence and requests for materials should be addressed to R.Q.T.