Chronic nitrogen deposition alters tree allometric relationships: implications for biomass production and carbon storage

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Abstract. As increasing levels of nitrogen (N) deposition impact many terrestrial ecosystems, understanding the potential effects of higher N availability is critical for forecasting tree carbon allocation patterns and thus future forest productivity. Most regional estimates of forest biomass apply allometric equations, with parameters estimated from a limited number of studies, to forest inventory data (i.e., tree diameter). However, most of these allometric equations cannot account for potential effects of increased N availability on biomass allocation patterns. Using 18 yr of tree diameter, height, and mortality data collected for a dominant tree species (*Acer saccharum*) in an atmospheric N deposition experiment, we evaluated how greater N availability affects allometric relationships in this species. After taking into account site and individual variability, our results reveal significant differences in allometric parameters between ambient and experimental N deposition treatments. Large trees under experimental N deposition reached greater heights at a given diameter; moreover, their estimated maximum height (mean ± standard deviation: 33.7 ± 0.38 m) was significantly higher than that estimated under the ambient condition (31.3 ± 0.31 m). Within small tree sizes (5–10 cm diameter) there was greater mortality under experimental N deposition, whereas the relative growth rates of small trees were greater under experimental N deposition. Calculations of stemwood biomass using our parameter estimates for the diameter–height relationship indicated the potential for significant biases in these estimates (~2.5%), with under predictions of stemwood biomass averaging 4 Mg/ha lower if ambient parameters were to be used to estimate stem biomass of trees in the experimental N deposition treatment. As atmospheric N deposition continues to increase into the future, ignoring changes in tree allometry will contribute to the uncertainty associated with aboveground carbon storage estimates across a forest with a large geographic distribution in eastern North America.

Key words: Acer saccharum; carbon allocation; diameter; height; mortality; nitrogen deposition; relative growth rate; temperate forests.

INTRODUCTION

Increased delivery of nitrogen (N) to natural ecosystems from anthropogenic sources might be expected to alter the growth and carbon (C) allocation patterns in forest trees. Nitrogen is often a growth-limiting nutrient in temperate forests, and, as a result, most tree species have evolved to rapidly respond to changes in soil N availability (Vitousek and Howarth 1991, LeBauer and Treseder 2008). An increase in the amount of N available to plants could then modify their growth and biomass allocation (Cheng and Zhong 2012, Vicca et al. 2012), which could plausibly shift patterns of forest C sequestration (Janssens and Luyssaert 2009, De Kauwe et al. 2014). Forest C storage is commonly estimated using allometric equations that use individual tree diameter, or

diameter and height, to estimate aboveground biomass (e.g., Jenkins et al. 2004, Saatchi et al. 2007, Picard et al. 2012). Therefore, any bias in parameter estimates due to a shift in allocation patterns in response to increased N availability could influence the outcome of those estimates. We studied the allometric relationships used to calculate stem biomass of a temperate tree species after 18 years of experimental N deposition and evaluated how those differences translate into estimates of biomass production and C storage in live trees.

As anthropogenic N deposition has increased, plant communities have responded in various ways, with consequential implications for forest C storage (Vitousek et al. 1997, Bobbink et al. 2010). Changes in plant physiology, biomass allocation, and mycorrhizal colonization have been reported as the result of increased N (Sefcik et al. 2007, Hyvöen et al. 2008, Xia and Wan 2008, Thomas et al. 2010). At a forest stand level, changes in individual production could have major effects on the capacity of forest ecosystems to store C in plant biomass

(Magnani et al. 2007, Sutton et al. 2008, Högberg 2011, but see Nadelhoffer et al. 1999). Thus, estimating shifts in plant growth and biomass allocation under future rates of atmospheric N deposition is critical to assess C storage in forests at local, regional, and global scales (Bonan 2008, Thomas et al. 2010).

Most estimates of tree biomass, growth, or forest dynamics are conducted using allometric equations that relate tree size to biomass, growth, and mortality (e.g., Niklas 1994, Dietze et al. 2008, Iida et al. 2014). The strong relationships among tree diameter, height, and growth rate have been widely used to estimate tree volume and biomass, as well as forest structure (e.g., Martin et al. 1998, Anfodillo et al. 2013). In addition, maximum individual biomass is closely related to forest biomass (Stegen et al. 2011); thus, reliable estimates of tree maximum growth potential are critical in the assessment of forest productivity. Tree size has also been used to infer demographic rates; for example, mortality can vary with size, decreasing as light limitation decreases with height, but also increasing at larger sizes due to individual senescence (King et al. 2006, Iida et al. 2014).

Besides the notable strength in the relationship between tree diameter and biomass within a tree species, there is still considerable variability in this relationship among life stages, individuals, populations, and geographic regions (Dietze et al. 2008). Intraspecific variability in growth and development varies as a function of the growing conditions (Niklas 1994, Anfodillo et al. 2013) and ontogeny (Peichl and Arain 2007). Stand differences in diameter–height and diameter–biomass relationships have been widely reported and often attributed to site conditions (e.g., stand density, soil fertility, water availability) or regional environmental gradients (e.g., temperature, precipitation; e.g., Shibuya et al. 2005, Watt and Kirschbaum 2011, Osada 2011, Feldpausch et al. 2011). Moreover, relative growth rate declines with tree size (Pregitzer and Euskirchen 2004, Mencuccini et al. 2005, Rose et al. 2009, but see Johnson and Abrams 2009), a trend that affects the rate of biomass accumulation in forest stands over time (Lichstein et al. 2009, Foster et al. 2014). Therefore, it is important to account for tree age and site-specific biases when using allometric relationships. However, these parameters are often estimated from limited data, without considering the range of variability associated with these relationships. In addition, most estimates of tree biomass are solely based on tree diameter (e.g., Ter-Mikaelian and Korzukhin 1997, Jenkins et al. 2004), ignoring the effects that soil fertility might have on tree height (Skovsgaard and Vanclay 2008). This lack of universal parameters and the scarcity of information about their potential variability across life stages and site conditions could potentially bias estimates of forest biomass and ecosystem C storage (Chave et al. 2005, Konopka et al. 2010), especially if they respond to human-induced environmental change (Fang et al. 2014).

We hypothesized that an increase in soil N availability, caused by anthropogenic N deposition, could alter allometric relationships in tree species. Presently, we are unaware of any study that has evaluated how changes in N availability might affect allometric relationships of forest species at a given location. Forest carbon allocation to growth varies with soil N availability (Vicca et al. 2012); in silvicultural stands, dominant tree height is strongly related to soil fertility (Skovsgaard and Vanclay 2008, García 2011); and, changes in basal area increment of several temperate tree species have been reported along gradients of anthropogenic N deposition (Boggs et al. 2005, Bedison and McNeil 2009). Because of potential self-shading, we also hypothesized that any changes in carbon allocation due to anthropogenic N will likely take place on the stem of a tree, instead of allocation being directed to growing more leaves and branches (Wolf et al. 2011a, Franklin et al. 2012). To test our hypotheses, we used 18 years of tree diameter, height, and mortality data collected for a dominant tree species in a long-term N deposition experiment. We evaluated changes in allometric relationships due to the increased availability of this growth-limiting element while still accounting for inter-site and individual variability in those relationships. We also used parameter estimates from the analysis of this data set to evaluate the potential bias in tree stemwood biomass estimates when the effects of experimental N deposition on allometric relationships are ignored. The specific questions we sought to answer were: (1) does the diameter–height relationship change with greater anthropogenic N deposition? If so, at which stages or sizes are these changes most prominent? (2) Does increased N availability have an effect on tree mortality? If so, does this effect vary with tree size? (3) Is the decrease in relative growth rate associated with tree size affected by future rates of atmospheric N deposition? (4) If allometric relationships vary with experimental N deposition, what is the bias in tree stemwood biomass estimates if these changes are not considered in the allometric equations? As atmospheric N deposition increases in the future, answering these questions will allow reducing the uncertainty associated with estimates of forest ecosystems C stocks.

METHODS

We estimated the effects of experimental N deposition on allometric relationships in sugar maple (*Acer saccharum* Marsh.), a dominant tree species in northeastern North America. In 1993, comparable forest sites were identified in four locations along the geographic distribution of northern hardwood forests in the Great Lakes Region (Michigan, USA; Table 1; MacDonald et al. 1993). At each site six plots (30 × 30 m) were delimited and the woody vegetation and soils were sampled. Stands are similar in age (currently ranging from 97 to 105 yr), in soil development (sand content ranges from 85% to 89%, pH from 4.47 to 5.03, and organic C from 15.4 to 19.4 mg C/g), and in forest composition (*A. saccharum* is the dominant tree species and is also common in all or some sites: *Quercus rubra*, *Fagus grandifolia*, *Tilia americana*,

TABLE 1. Study locations in Michigan, USA along a latitudinal gradient in the Great Lakes Region of North America, climatic conditions (mean temperature and annual precipitation) and total ambient nitrogen deposition at each location.

Locations	Coordinates	Temperature (°C)	Precipitation (mm)	N deposition ($g·m^{-2}·yr^{-1}$)
A (most northern)	46°52′ N 88°53′ W	4.8	821	0.68
B (northern)	45°33′ N 84°52′ W	6.1	828	0.91
C (southern)	44°23′ N 85°50′ W	6.9	856	1.17
D (most southern)	43°40′ N 86°09′ W	7.6	793	1.18

Acer rubrum, and *Prunus serotina*; Zak et al. 2006). The main differences among sites are climatic, with mean annual temperature increasing from the most northern site to the most southern site; total annual precipitation is comparable among the three most northern sites (Table 1). Ambient N deposition increases from north to south (Table 1). In 1994, half of the plots at each site ($n = 3$) started receiving experimental N deposition, simulating the rate of atmospheric N deposition anticipated for eastern North America at the start of the experiment (Bredemeier et al. 1998, Fenn et al. 1998; +3 g NO_3^- –$N·m^{-2}·yr^{-1}$ over ambient levels [Table 1]). Nitrogen has been added since then in six applications during the growing season (0.5 N g/m^2 monthly) as solid $NaNO_3$. At each of the sites, the remaining plots ($n = 3$) only received ambient N deposition (Table 1).

Study species and vegetation measurements

All trees with a diameter at breast height (1.37 m) ≥ 5 cm were identified to the species and individually numbered. Their diameters at breast height (*D*) were measured each year (1993–2011) during the dormant period (i.e., before spring leaf-out) using tapes; trees dying during the previous year were also noted. In 1998 and 2005, tree heights were measured from two directions, ~180° apart, using clinometers. *A. saccharum* is the dominant tree species at each site, with overall stand and *A. sacchrarum* biomass averaging 261 and 237 Mg/ha, respectively, at the most northern site (A), 261 and 224 Mg/ha at the northern site (B), 274 and 216 Mg/ha at the southern site (C), and 234 and 166 Mg/ha at the most southern site (D; Zak et al. 2006). *A. saccharum* is a shade-tolerant and slow-growing species that mainly occurs in mesic and fertile deciduous forests. It is a large tree that can reach 18–35 m in height and 60–120 cm in diameter; the trunk is relatively straight with branches in the last two thirds of its length (Barnes and Wagner 2004).

Allometric relationships

For our analyses, we explored common allometric equations adding different combinations of fixed and random effects. Here, we report on the final models, which were selected according to the Deviance Information Criterion (DIC, models with lowest DIC best fit the data [Spiegelhalter et al. 2002]; see Appendix S1 for a list of models tested).

Diameter–height

We analyzed the allometric relationship between tree height, *H*, and diameter, *D*, for 943 individuals at two times (1998 and 2005). We estimated height of individual *i* at time *t* as an asymptotic function of diameter using a two-parameter equation proposed by Thomas (1996; also see Iida et al. 2011): $H_{it} = a(1 - \exp(-bD_{it}))$. Parameter *a* represents the maximum height a tree could reach, and parameter *b* estimates the rate of decrease in height growth with increasing diameter. We modified this basic equation to account for different sources of uncertainty (Clark 2005, 2007*a*). For example, we included variability attributed to N deposition treatment (ambient vs. experimental N deposition) in the estimation of the parameters (*a*, *b*). Additionally, variability due to differences in site conditions (mainly climate, but also soil N content or atmospheric N deposition [Table 1], or any other site characteristics that could affect tree performance) was accounted for by adding site-specific fixed effects (SFE). We centered around their mean ($\overline{SFE}$) to improve convergence and facilitate interpretation of the results (Gelman and Hill 2007). To account for individual variability in the response, due to individual differences other than those associated with diameter (e.g., genetic differences, status in the canopy, competitive pressure, etc.), we also included individual-level random effects (IRE) (Clark et al. 2003, 2007*b*). For individual *i* at time *t*:

Likelihood

$$H_{it} \sim \text{Normal}(Hm_{it}, \sigma^2)$$

Process model

$$Hm_{it} = a_{\text{treatment}(i)} \left(1 - \exp \left(-b_{\text{treatment}(i)} D_{it} \right) \right) + \left(SFE_{\text{site}(i)} - \overline{SFE} \right) + IRE_i$$

To calculate this large number of parameters, we followed a Bayesian approach (Gelman and Hill 2007) and estimated parameters from prior distributions. Parameters for each treatment were estimated from slightly informative distributions, $a_* \sim \text{Uniform}(15, 45)$ and $b_* \sim \text{Uniform}(0.01, 0.1)$. We constrained the range of variability to a range of values commonly reported for these parameters (Barnes and Wagner [2004] for tree maximum height, Iida et al. [2011] for rate of decrease in height growth), but still large enough to allow the data

to inform the estimates; this approach enabled faster convergence in the analysis. Site and individual effects were estimated from non-informative distributions, SFE_* ~ Normal(0, 100) and IRE_* ~ Normal(0, σ^2_{IRE}). Variances were estimated as $1/\sigma^2, 1/\sigma^2_{IRE}$ ~ Gamma(0.01, 0.01).

Diameter–mortality

We modeled the size-dependent probability of mortality by analyzing annual mortality data, from 1994 to 2011, as a function of tree diameter from the census conducted in the previous year. We have records for 1566 trees; of those 502 died during the 18-yr period of this study. We used a Cox survival model that includes hazard and the risk (Andersen and Gil 1982) and analyzed risk as a function of tree diameter. The data for each tree and year was coded as $N_{it} = 0$ if alive and $N_{it} = 1$ if found dead that year. The data set was then modeled as a count process. Again, we included site-specific fixed effects (SFE). For individual i at time t:

Likelihood

$$N_{it} \sim \text{Poisson}(\lambda_{it})$$

Process model

$$\lambda_{it} = \text{hazard}_t e^{\text{risk}_{it}}$$

Parameter model

$$\text{risk}_{it} = a_{\text{treatment}(i)} + b_{\text{treatment}(i)} \ln(D_{it})$$
$$+ c_{\text{treatment}(i)} D_{it} + \left(\text{SFE}_{\text{site}(i)} - \overline{\text{SFE}}\right)$$

As with the previous analysis, we estimated model parameters from prior distributions. Hazard represents differences in mortality year to year, likely due to environmental conditions in each particular year; hazard_t ~ Gamma(1, 1). Risk was estimated as a function of diameter and SFE; parameter a represents mortality rates at very small diameters, and parameters b and c represent the size-dependent effect on mortality, a_*, b_*, c_* ~ Normal(0, 10000). Site fixed effects were estimated as SFE_* ~ Normal(0, 100).

Diameter–relative growth rate

Annual radial relative growth rate (RGR) for 1994–2011 was calculated as the difference in log-transformed tree diameter from one census to the next, $\text{RGR}_t = \ln(D_t) - \ln(D_{t-1})$). For our analyses, we discarded estimates of RGR that were zero or negative as being the result of measurement error. This could create a positive bias in RGR values, but as our intent was to compare the two treatments, we assumed the biases to be similar (33% of data points from ambient plots and 30% from N deposition plots were not used). That left us with a total of 13373 records distributed among 1079 individuals. RGR is commonly analyzed as a linear function of log-transformed tree diameter; we also added site fixed effects,

SFE, and individual random effects, IRE. In this case, we modeled the variance associated with each of the RGR_{it} records, σ^2_{it}, as a function of tree diameter. Variability along tree allometric relationships usually shifts with tree size (Fig. 1C) and can be estimated as a function of tree diameter (Lines et al. 2012). For individual i at time t:

Likelihood

$$\text{RGR}_{it} \sim \text{Normal}(\text{RGRm}_{it}, \sigma^2_{it})$$

Process model

$$\text{RGR}_{it} = a_{\text{treatment}(i)} - b_{\text{treatment}(i)} \ln(D_{it})$$
$$+ \left(\text{SFE}_{\text{site}(i)} - \overline{\text{SFE}}\right) + \text{IRE}_i$$

Parameter model

$$\ln(1/\sigma^2_{it}) = \mu_1 + \mu_2 \ln(D_{it})$$

To aid with convergence of the parameter estimates, we constrained some of the prior distributions to be positive, a_*, b_*, μ_* ~ Normal(1, 10 000), because these parameters are always positive in nature. Site fixed effects and random individual effects were estimated as described previously, SFE_* ~ Normal(0, 100), IRE_* ~ Normal(0, σ^2_{IRE}) and $1/\sigma^2_{IRE}$ ~ Gamma(0.01, 0.01).

All analyses were performed in OpenBUGS (Thomas et al. 2006), and, after a burn-in period, parameter posterior estimates (means, standard deviation, and 95% credible intervals [CI]) were derived from three converging chains thinning every 100th iteration. We used these estimates to predict height, mortality, and relative growth rate as a function of diameter by running 10000 additional iterations and reporting predicted values (means and 95% predicted intervals [PI]). The uncertainty associated with these predictions (95% PI), reflects both uncertainty in parameter estimates and uncertainty attributed to site and individual differences.

Biomass estimation

We then quantified the potential bias in aboveground stemwood biomass estimates that could occur if the effects of experimental N deposition on allometric relationships were ignored. We estimated stemwood biomass in all the plots for each of the four sites (an area of 0.27 ha per treatment and site) based on the trees diameters in 2005 (one of the 2-yr heights were directly measured and 11 yr into the experimental N deposition treatment), and based on: (1) actual height data from 2005 (2) estimated 2005 height using ambient parameter values (mean and 95% CI), or (3) estimated 2005 height using experimental N deposition parameter values (mean and 95% CI). We used an equation that includes both tree diameter and height to calculate stemwood biomass as a function of tree diameter (D, cm) and height (H, m): Dry biomass (kg) $= \beta_1 D^{\beta_2} H^{\beta_3}$ where parameter values specific for *A. saccharum* are β_1, 0.0301; β_2, 2.0313; and β_3, 0.8171 (Lambert et al. 2005). The dry mass of leaves, branches, and bark was excluded from our analyses.
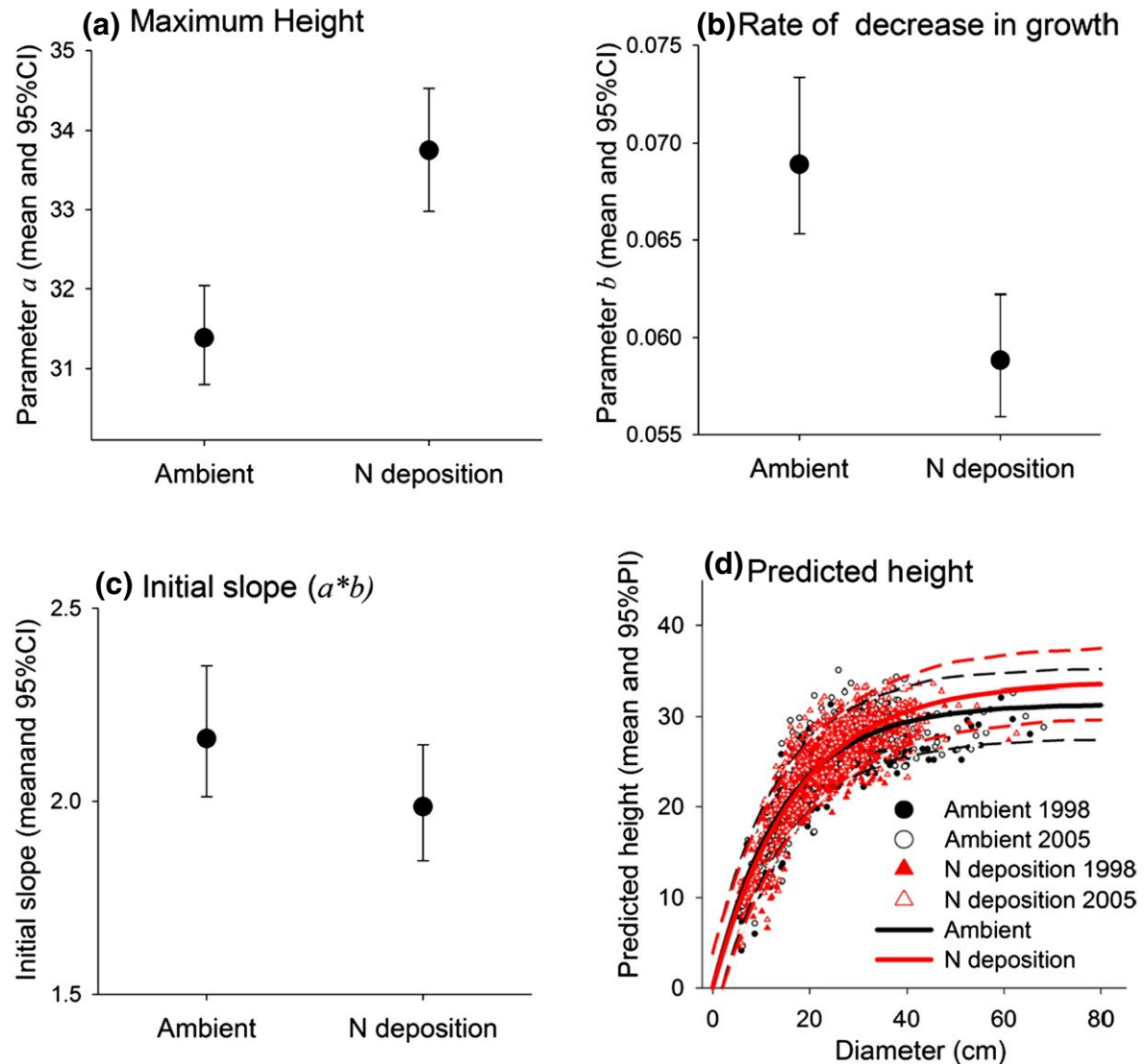
FIG. 1.   Results from the diameter-height analysis. (a) Posterior mean estimates, and 95%CI, of the asymptote parameter for tree maximum height. (b) Posterior mean estimates, and 95%CI, of the slope parameter describing the decrease in height growth rate with increasing diameter. (c) Estimates of the initial slope (mean and 95%CI) in the height-diameter curve. (d) Predicted height in m (means solid lines and 95% predicted interval [PI] dashed lines) as a function of tree diameter, points represent the data. Parameters are considered significantly different between treatments if their 95%CI do not overlap.

Although Lambert et al. (2005) reported parameter means, standard errors, and error term variance, we only used the mean parameter values in the simulations. Therefore, uncertainty associated with our stemwood biomass estimates, is only due to the uncertainty, from parameters and individuals, we quantified in our analyses.

RESULTS

Here, we report results for the main parameters associated with each of the three allometric relationships; additional parameters (i.e., site fixed effects, variances, and parameters associated with the estimation of variances) are reported in Appendix S1. We assessed

statistical significance by comparing the 95% credible intervals (CI) around parameter estimates; ambient and experimental N deposition treatments were considered significantly different when their 95% CIs did not overlap. Tree diameters ranged between 5 and 70 cm, and heights varied between 2 and 39 m. Most mortality took place among small individuals; the largest tree reported dead during the study period was 37.5 cm in diameter. Annual RGRs ranged from 0.0007 to 0.0763 mm.

Diameter–height

Parameters defining the tree height–diameter relationship differed between the two treatments. The

parameter representing maximum height, *a*, was greater under experimental N deposition, with means differing between treatments by more than 2.5 m (Fig. 1A). The rate of decrease in height growth with increasing diameter, parameter *b*, was lower under experimental N deposition (Fig. 1B). However, when we estimated the initial slope of the curve, *a·b*, this did not differ between treatments, although the estimate was slightly lower under experimental N deposition (Fig. 1C). Predicted height curves, as a function of diameter, reveal a large overlap between the two treatments and encompassed most of the variability observed in the data (Fig. 1D).

Diameter–mortality

The analysis of mortality as a function of tree size, (i.e., diameter) also revealed differences between N deposition treatments. The intercept parameter, *a*, a proxy for mortality at small tree sizes, was significantly higher under experimental N deposition (Fig. 2A). The first slope parameter, *b*, was higher and significantly different from zero for the ambient treatment (95% CI did not overlap zero); whereas, the slope for the experimental N deposition treatment did not differ from zero (Fig. 2B). The second slope parameter, *c*, was negative and different from zero for each treatment. The values were also significantly different from each other, wherein the experimental N deposition treatment had a higher, less negative, value (Fig. 2C). Hazard estimates varied year to year reflecting differential mortality during the period of time the study took place (1994–2011; Fig. 2D). Predicted mortality during the first year of the experiment (1994) was relatively low and did not differ between treatments (Fig. 2E). However, when we estimated mortality for the entire study period (18 yr), mortality rates were mainly concentrated on small tree sizes. Also, at small tree sizes, the two treatments differed, with greater mortality under experimental N deposition (Fig. 2F).

Diameter–relative growth rate

The analysis of radial RGR as a function of tree diameter showed that growth rates at small diameter sizes, parameter *a*, were higher under experimental N deposition (Fig. 3A). But as the RGR were similar between the two treatments at large diameter sizes, the rate of decrease in RGR with diameter was also greater under experimental N deposition (Fig. 3B). Predicted curves of tree RGR as a function of diameter reveal the overlap between treatments, due to the large variability of the data, but also show a decrease in differences between N deposition treatments with increasing tree sizes (Fig. 3C).

Biomass estimation

We calculated aboveground stemwood biomass using the actual diameter and height data collected in 2005

(year when heights were directly measured). Stem biomass estimated in the experimental N deposition plots for 2005 was 183 Mg/ha for site A (most northern), 167 Mg/ha in site B (northern), 140 Mg/ha for site C (southern), and 152 Mg/ha at site D (most southern; Appendix S2 for ambient plots estimates). We then proceeded to compare those values (i.e., from actual diameter and height data) with biomass estimates calculated using ambient and experimental N deposition parameters from the diameter–height relationship (i.e., from 2005 diameter data and 2005 height estimates using allometric equations). Estimates for the N deposition plots using ambient parameters were (mean [95%PI]): 179 (177, 182) Mg/ha in site A, 163 (160, 165) Mg/ha in site B, 137 (135, 139) Mg/ha in site C, and 143 (143, 148) Mg/ha for site D. When using the experimental N deposition parameters estimates of stem biomass were (mean [95%PI]): 184 (180, 187) Mg/ha in site A, 166 (163, 169) Mg/ha in site B, 139 (136, 141) Mg/ha in site C, and 149 (146, 152) Mg/ha for site D. Estimates using the ambient parameters systematically underestimated stem biomass in all four sites, estimates using N deposition parameters did not differ from those of the data in three of the sites and underestimated biomass in site D (most southern). The biases associated with using the "wrong" N treatment parameters (i.e., experimental N deposition parameters for the ambient plots and ambient parameters for the experimental N deposition plots) would translate into a statistically significant overestimate of stem biomass in three of the four sites for the ambient plots (95% CI do not overlap zero; Fig. 4A) and a significant underestimate of stem biomass at the four sites for the experimental N deposition plots (Fig. 4B).

Discussion

Estimates of forest carbon stocks are usually associated with considerable levels of uncertainty (Butt et al. 2013, Holdaway et al. 2014). Likely, one of the many factors contributing to these biases is the use of allometric equations developed under specific conditions to estimate biomass at sites subjected to a different environment (Chave et al. 2005, Ishihara et al. 2015). Thus, accounting for differences in allocation patterns by using environment-specific allometric relationships could potentially reduce biases in biomass estimates. In particular, future rates of anthropogenic N deposition could alter plant productivity and carbon allocation patterns, shifting the amount of biomass sequestered in forests and thereby globally influencing the amount of anthropogenic CO_2 stored within these ecosystems (Gruber and Galloway 2008, Heimann and Reichstein 2008). Using standard allometric equations, our results indicate significant differences in allometric parameters, particularly in tree height, between trees growing under ambient and experimental N deposition (a difference of ~2.3 m in maximum tree height). Here, we demonstrate that ignoring the effects of anthropogenic N deposition on tree biomass
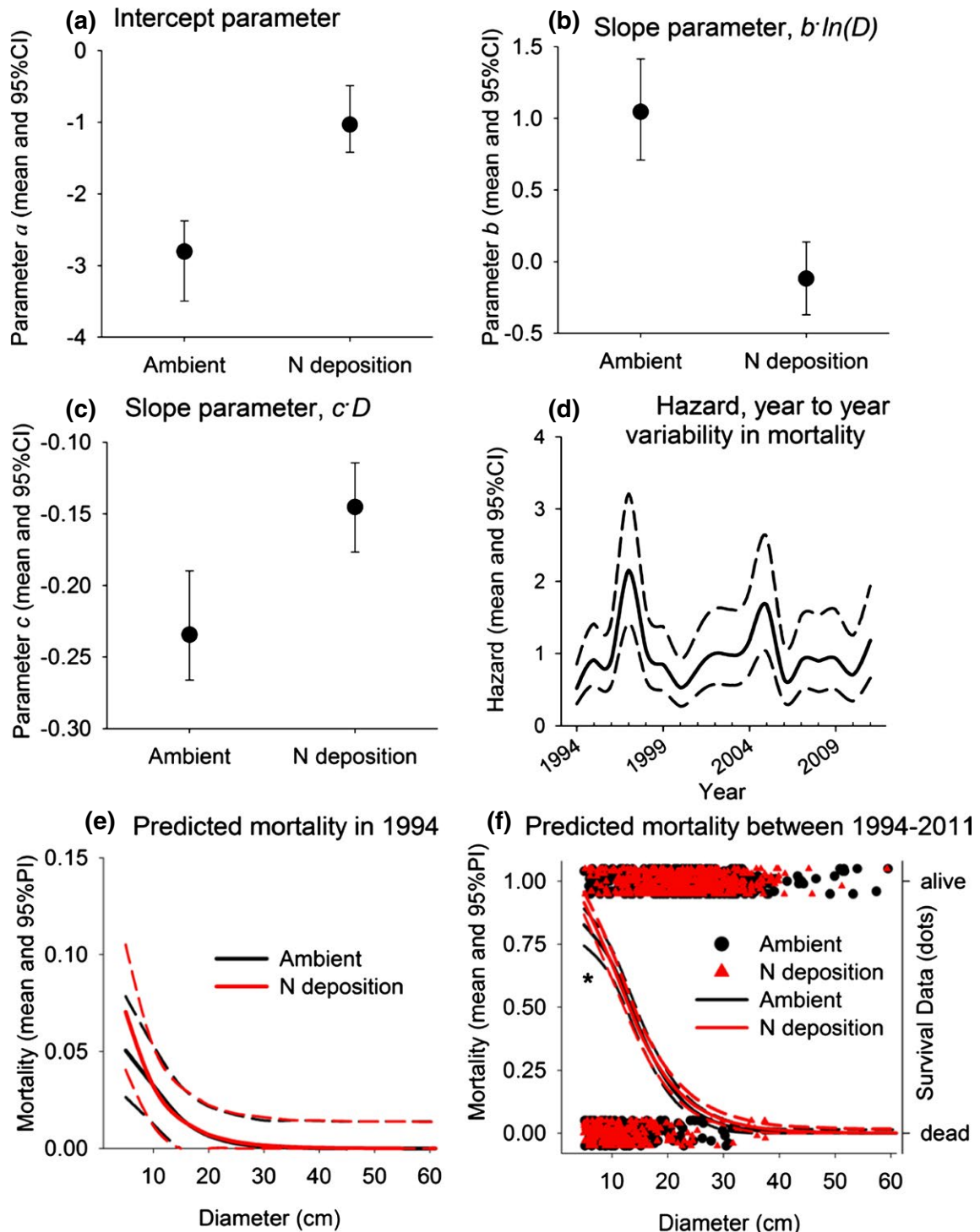
FIG. 2. Results from the diameter-mortality analysis. Posterior mean estimates and 95%CI of (a) the intercept parameter, representing mortality rates a very small diameters, (b) of the slope parameter describing the decrease in mortality with increasing ln(D), and (c) of the slope parameter describing the decrease in mortality with increasing diameter (D). Also shown are (d) estimates of the hazard (mean solid line and 95%CI dashed lines), representing year-to-year changes in mortality not related to tree size. Predicted probability of mortality (means solid lines and 95%PI dashed lines) is shown as a function of tree diameter during (e) the first year of the experiment, and (f) during the 18-yr study period (points represent the data; asterisk indicates 95%PI do not overlap at that diameter size). Parameters are considered significantly different between treatments if their 95%CI do not overlap.
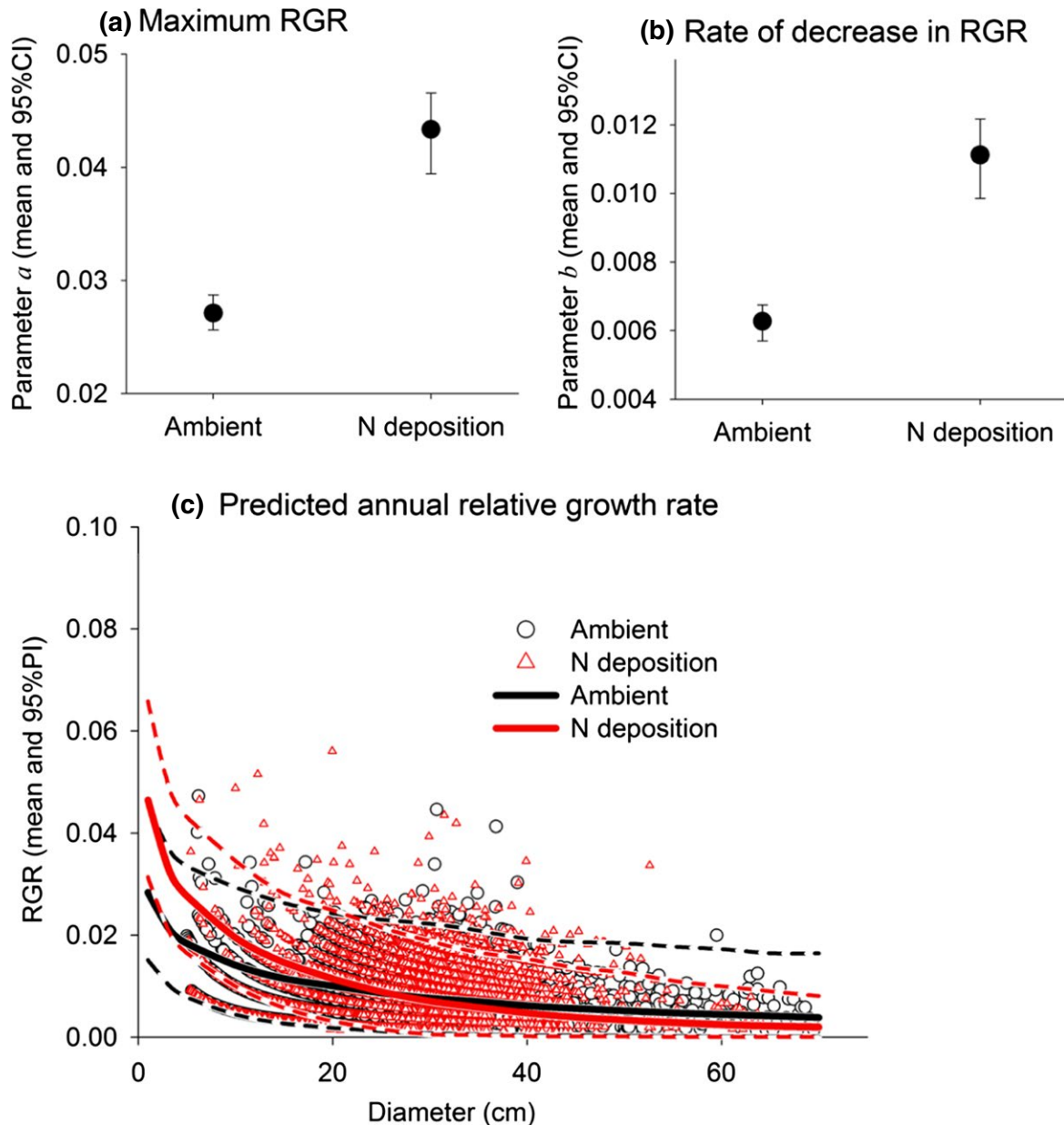
INÉS IBÁÑEZ ET AL.

FIG. 3. Results from the diameter-radial relative growth rate (RGR) analysis: (a) posterior mean estimates and 95%CI of the intercept parameter, representing the maximum growth rates for small trees, (b) posterior mean estimates and 95%CI of the slope parameter describing the decrease in RGR with increasing diameter, (c) predicted RGR (means solid lines and 95%PI dashed lines) as a function of tree diameter, points represent the data. Parameters are considered significantly different between treatments if their 95%CI do not overlap.

allocation can significantly bias estimates of forest stemwood biomass by 4 Mg/ha (~2.5% bias). These differences would have gone undetected if the parameters derived under ambient N deposition had been used to estimate stem biomass in the experimental N deposition treatment.

Most regional estimates of forest biomass are conducted by applying allometric equations to forest inventory data (Caspersen et al. 2000, Thomas et al. 2010). Parameters for these equations are usually estimated from a limited number of studies (Jenkins et al. 2004), missing potential biases due to specific growing conditions associated with each site (Saatchi et al. 2007, Watt and Kirschbaum 2011). Because N availability limits plant growth in most forests (Vitousek and Howarth 1991), current rates of anthropogenic N deposition could have a significant impact on the productivity of these ecosystems. Under high nutrient conditions
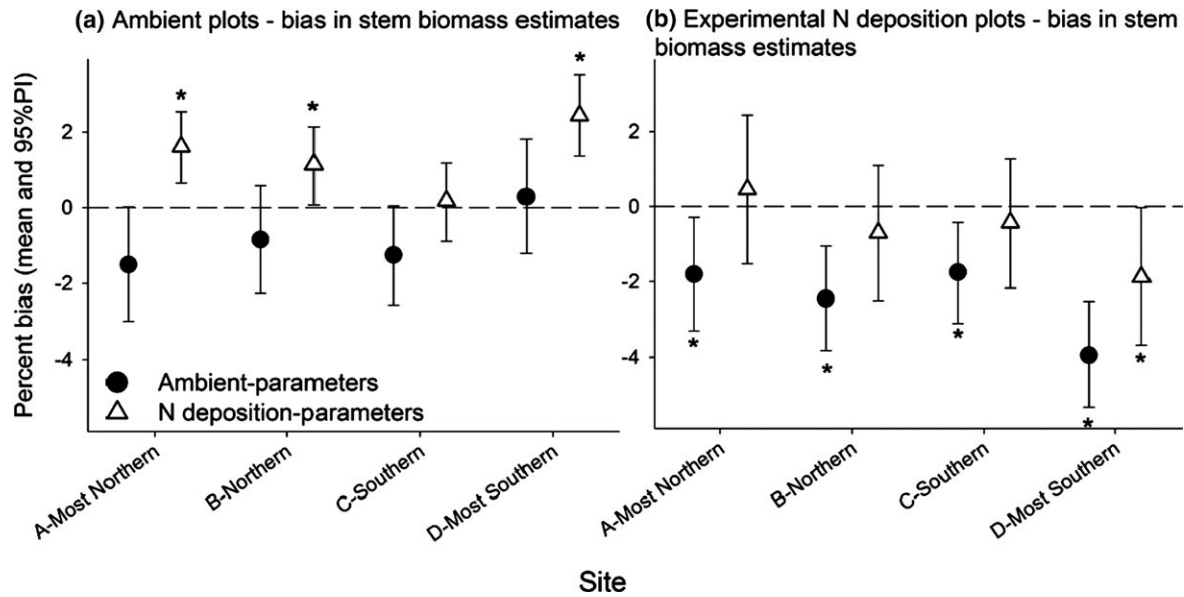
FIG. 4. Results from the bias calculations of stem biomass estimates as a function of tree diameter and height using ambient and N deposition parameters (points) with respect to direct estimates from diameter and height data (horizontal line), for (a) ambient plots and (b) experimental N deposition plots. Biases are considered statistically significant (indicated by an asterisk) if their 95%PI do not overlap the zero line (data value).

plants often invest more in aboveground biomass (Chapin 1980, Xia and Wan 2008); therefore, it should not be surprising that C allocation patterns of trees, and the allometric relationships that estimate biomass, would change with greater rates of anthropogenic N deposition. Also, when light is limited, as it usually is in forest stands, leaf area has been maximized and likely there is a greater allocation to woody biomass at the expense of leaves (Wolf et al. 2011*a*); therefore, shifts in biomass allocation probably take place in stems rather than leaves and branches (Franklin et al. 2012), a response that is consistent with the increase in stem biomass under experimental N deposition we report here.

Does the diameter–height relationship change with increasing N deposition? If so, at which stages or sizes are these changes most prominent?

Most estimates of tree biomass are based solely on diameter measurements (Jenkins et al. 2004); however, including height can reduce error estimates by 50% (Feldpausch et al. 2012). In particular, tropical forest biomass is overestimated if height is not taken into account, affecting calculation of C stocks and emissions (Marshall et al. 2012). Maximum height is also a good predictor of tree allometry (Osada 2011) and maximum tree biomass is strongly correlated to forest biomass (Stegen et al. 2011). In our analyses, we found that the main difference between our two treatments was in the estimate of maximum tree height, which was greater under experimental N deposition (Fig. 1A). This would translate into a greater accumulation of stem biomass

per unit of time as anthropogenic N deposition increases. There was also a lower decrease in the rate of height growth with increasing diameter (Fig. 1B) under experimental N deposition, revealing lower constraints on height growth, which became apparent in the larger diameter classes (i.e., >30 cm; Fig. 1D). These results indicate that future rates of atmospheric N deposition would allow *A. saccharum* trees to attain a taller stature at a given diameter, and thus accumulate more biomass in their stems. From the site-index point of view, the differences in height reported for this species (~2.3 m) would amount to a change in site index of more than six units (from 74 to slightly more than 80 [estimates for 100-year-old trees]; Carmean et al. 1989).

Does increased N availability have an effect on tree mortality? If so, does this effect vary with tree size?

Estimates of stand biomass also depend on the age structure of the forest, and demographic rates can also be estimated as a function of tree size. Tree mortality rates are high at small tree sizes and younger ages, mainly due to competitive interactions with the canopy trees. Carbon starvation due to insufficient irradiance has been frequently reported as the major cause of sapling mortality in temperate forests (Canham et al. 1999, Kobe 2006). Our study was not an exception; the majority of mortality occurred among smaller individuals (Fig. 2B). Mortality can also increase at the largest sizes, but in this case, it is attributed to senescence and an age-related growth decline of the oldest individuals (Foster et al. 2014). However, our data did not include mortality of any individual more

than 40 cm in diameter. This was not surprising because these stands are ~100 years old and *A. saccharum* can live several hundred years (~300; Loehle 1988). Thus, it is difficult to infer future population dynamics given our data. But, what our data revealed is that, under experimental N deposition, mortality in small trees was higher than those under ambient conditions (Fig. 2A). We infer that higher mortality of small size trees under experimental N deposition may be due to increased relative growth rates at small diameter sizes (see following section). Furthermore, saplings with larger biomass would have higher maintenance costs that could not be met under the forest canopy (Canham et al. 1999, Ogle and Pacala 2009). In summary, experimental N addition may be accelerating stand development, wherein saplings grow faster, but mortality also thins smaller individuals (likely suppressed) at a faster rate.

In our study, we did not have sufficient mortality to test whether chronic N deposition may also shift mortality rates at large-diameter sizes, although the analysis of forest inventory data in North America revealed no association between atmospheric N deposition and mortality rates for this species (Thomas et al. 2010). Mortality also fluctuated year to year (Fig. 2D). The peak in mortality during 2005 could be explained by the particularly dry conditions that summer (data not shown; Brown et al. 2000), and unusually low temperatures in May could be associated with low growth rates and consequentially higher mortality in 1997 (air mean monthly temperature was between 3.16°C and 4°C lower that year than the average of the study period [Brown et al. 2000]).

Is the decrease in relative growth rate associated with tree size affected by future rates of atmospheric N deposition?

To accurately predict forest productivity over time, tree growth models must account for size- and age-specific differences on biomass production. In particular, the decline in relative tree growth (RGR) associated with tree size is critical to estimate productivity along the successional process (Peichl and Arain 2007, Konopka et al. 2010). Our analyses reveal large variability in RGR at a given diameter and a wide overlap between N deposition treatments. Estimates of RGR are highly correlated with light availability (Niinemets 1998); thus, incorporating individual random effects, as we did here, helped to account for this variability and to better assess the difference between the two treatments, illustrating how N deposition changed RGR along tree sizes. Even if the high variability among individuals caused overlap between treatments, parameter estimates differed between them. Trees under experimental N deposition had higher RGR at small-diameter sizes than those under ambient N deposition, this trend could have been due to lower belowground investment as N becomes less limiting for tree growth (Peichl and Arain 2007, Wolf et al. 2011a, Franklin et al. 2012). The association

between higher mortality rates and higher RGR at small diameter sizes in the experimental N deposition plots could be explained by a delayed cost of earlier rapid growth. Excess growth would have caused higher respiratory costs or lower leaf area per unit of living biomass, compromising sapling survival (Rose et al. 2009).

The two treatments had similar radial RGR at large diameter classes, thus the accelerated decrease in RGR under experimental N deposition. This finding indicates that trees are getting bigger faster when grown at higher N levels. These results, together with the reported increase in tree height at a given diameter (see previous section) confirm previous analyses where, at the stand level, biomass accumulates faster under experimental N deposition (Pregitzer et al. 2008). However, with our data and study system (~100-year-old stands), we are not able to assess if stemwood biomass is just accumulating faster or if the experimental N deposition treatment will also increase the total amount of stemwood biomass accumulated in the long term. Still, our result, faster rate of biomass accumulation, is quite relevant as most forests in the region are being harvested before they reach old growth status and, at least in the earlier stages, the rate of carbon sequestration seems to be affected by N deposition.

If allometric relationships vary with experimental N deposition, what is the bias in tree biomass estimates if these changes are not considered in the allometric equations?

Ecosystem estimates of C storage are not only dependent on allocation and turnover process but also on the sensitivity of these processes to resource limitation (Thomas et al. 2013, De Kauwe et al. 2014). Furthermore, ecosystem models of the carbon cycle also take into consideration allometric constraints when estimating the capacity of the vegetation to store carbon (Wolf et al. 2011b). Using our treatment-specific allometric parameters, we found a statistically significant bias, ranging from −3.94% to −1.75%, in the estimation of aboveground stemwood biomass, supporting previous analyses of increased stand growth under the N deposition treatment by Pregitzer et al. (2008). Thus, these findings could clarify some of the uncertainties surrounding the relationship between atmospheric N deposition and forest C storage (Sutton et al. 2008). Moreover, the experimental N deposition treatment only took place over the last 20 years of these 100-year-old stands, therefore, the reported differences could be exacerbated in stands exposed to higher levels of N deposition during their full lifespan.

Conclusions

Gradient-based studies of the effects of N deposition on forests have revealed differential growth among tree

species, but their estimates are limited due to the confounding effects of other environmental factors, e.g., temperature, precipitation, soil conditions, tropospheric ozone, that could also affect plant productivity and alter the effect of atmospheric N deposition (Ollinger et al. 2002, Bedison and McNeil 2009, Solberg et al. 2009). Our experiment, replicated at four locations along a climatic gradient, minimized that issue and provided an assessment of the specific effects of chronic N deposition on aboveground stemwood biomass allocation. In addition, incorporating a site-specific term in our analyses allowed us to account for any potential bias due to the characteristics of each geographic location (climate, soils, pollution; Stegen et al. 2011), and, moreover, including individual random effects allowed us to account for variability among individuals due to factors we did not observe (genetic differences, competitive ability, status in the canopy). Our results, indicating greater maximum tree height at larger size classes and a faster rate of stemwood biomass accumulation, point to a potentially important response to anthropogenic N deposition. The higher mortality rates and higher growth rates at small tree sizes in the experimental N deposition treatment could be indicating accelerated development of these stands. However, as these stands are relatively young (~100 years) and our study species is a long-lived tree (~300 years), we are far from being able to differentiate between accelerated development and actual increases in size. Regardless of the mechanism involved, ontogenetic acceleration or actual larger sizes, the main conclusion of our work is that the most common method used to estimate tree stem biomass, i.e., using allometric relationships derived under ambient conditions, would be biased if used for regions experimenting high levels of anthropogenic N deposition. As increasing levels of anthropogenic N deposition have become more prevalent in most terrestrial ecosystems, understanding the potential effects of greater N availability on tree species will be critical for forecasting future forest productivity and the potential of northern temperate forests to function as a globally important sink for anthropogenic CO_2 in the Earth's atmosphere.

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SUPPORTING INFORMATION

DATA AVAILABILITY