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**Anthropogenic nitrogen deposition ameliorates the decline in tree growth
caused by a drier climate**

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Abstract. Most forest ecosystems are simultaneously affected by concurrent global change drivers. However, when assessing these effects, studies have mainly focused on the responses to single factors and have rarely evaluated the joined effects of the multiple aspects of environmental change. Here, we analyzed the combined effects of anthropogenic nitrogen (N) deposition and climatic conditions on the radial growth of *Acer saccharum*, a dominant tree species in eastern North American forests. We capitalized on a long-term N deposition study, replicated along a latitudinal gradient, that has been taking place for more than 20 years. We analyzed tree radial growth as a function of anthropogenic N deposition (ambient and experimental addition) and of summer temperature and soil water conditions. Our results reveal that experimental N deposition enhances radial growth of this species, an effect that was accentuated as temperature increased and soil water became more limiting. The spatial and temporal extent of our data also allowed us to assert that the positive effects of growing under the experimental N deposition are likely due to changes in the physiological performance of this species, and not due to the positive correlation between soil N and soil water holding capacity, as has been previously speculated in other studies. Our simulations of tree growth under forecasted climate scenarios specific for this region also revealed that although anthropogenic N deposition may enhance tree growth under a large array of environmental conditions, it will not mitigate the expected effects of growing under the considerably drier conditions characteristic of our most extreme climatic scenario.

Key words: Acer saccharum*; diameter growth; drought; fertilization effect; global warming; lag effects; Northern hardwood forest; physiological response; sugar maple*

Introduction

The widespread increase in nitrogen (N) deposition from anthropogenic activities has exposed forests worldwide to levels of N unprecedented in the evolutionary history of forest plants (Vitousek and Howarth 1991, Chadwick et al. 1999). Because plant species have adapted to deal with a chronic scarcity of this resource, and to rapidly respond to changes in soil N availability, the impacts of anthropogenic N on plant performance are far reaching (Xia and Wan 2008, LeBauer and Treseder 2008, Bobbink et al. 2010). Furthermore, anthropogenic N deposition is not taking place in isolation; changes in temperature and precipitation are also impacting forest

ecosystems and are likely to interact with the effects of anthropogenic N deposition on forest growth (Ollinger et al. 2002, Suddick et al. 2013, Kobe et al. 2014). In particular, warming temperatures and a greater likelihood of extended drought, two major forest stressors in the near future (Vose et al. 2016, Hember et al. 2017), will likely interact with the effects of N deposition on plant species. However, we have conflicting knowledge about how these combined factors might affect the functioning of forest ecosystems (Solberg et al. 2009, De Marco et al. 2014). In order to then assess the future impact of anthropogenic N deposition and climate change on tree species we investigate how trees exposed to *ca.* 20 years of experimental N deposition responded to varying environmental conditions.

Anthropogenic N emissions to the atmosphere increased the availability of this growth-limiting nutrient in forest ecosystems across the Earth (Vitousek et al. 1997, Talhelm et al. 2012). Although some of these emissions (NO_x) have declined during the last few decades, emissions of non-regulated forms (NH_3) have been increasing (Li et al. 2016). Therefore, ecosystems will continue to be exposed to unparalleled levels of N availability, which could plausibly elicit both positive and negative effects on forests. Negative tree growth responses to increasing N deposition are mostly associated with greater soil acidity as well as the leaching of phosphorous and base cations (Izuta et al. 2004, Perakis et al. 2006, Zaccherio and Finzi 2007). In contrast, anthropogenic N deposition often has a 'fertilization effect' on tree species and positively affects growth (e.g., Spinnler et al. 2003, Solberg et al. 2009, Vicca et al. 2012, Ferretti et al. 2014), maximum tree height (Ibáñez et al. 2016), as well as carbon storage in trees and soils (e.g., Pregitzer et al. 2008, Hyvöen et al 2008, Thomas et al. 2010). However, this fertilization effect appears to be mediated by other environmental factors (Magnani et al. 2007). For example, in a tree growth study across an environmental gradient, Bedison and McNeil (2009) speculate that temperature, N saturation, soil acidity and ozone, could be offsetting some of the growth-enhancing effects of anthropogenic N.

Temperate forests will also experience warming and a greater incidence of drought in the near future (Klos et al. 2009, Clark et al. 2016, Lienard et al. 2016). Although tree species vary in their responses, radial growth appears to be highly sensitive to water limitation (e.g., Adams and Kolb 2005, Jump et al. 2006, Brzostek et al. 2014). In the case of isohydric species, like *Acer saccharum*, the most immediate response to low soil water availability is the closure of stomata to better maintain a constant level of leaf turgor (Manzoni et al. 2013). If drought remains for

long periods of time, the major effect is decreased photosynthetic assimilation and reduced radial growth (Bahari et al. 1985). In extreme cases, this could then lead to carbon starvation and increased risk of death (McDowell et al. 2008). Thus, understanding tree species performance under warmer and dryer conditions becomes essential for forecasting productivity in forests into the future.

Most studies investigating the combined effects of anthropogenic N deposition and soil water availability on tree growth have followed one of two approaches. Experimental studies, mainly conducted with seedlings and saplings under controlled conditions in greenhouses, report a detrimental effect of greater N availability when plants are grown under water-limited conditions (DeVisser et al. 1996, Dziedek et al. 2016). The mechanism behind this response is greater leaf area promoted by high N availability that cannot be sustained under dry soil conditions (Nilsen 1995). In contrast, observational studies, mainly focused on adult tree growth along environmental gradients of soil N and water availability, report a positive relationship between increased N availability and resilience to drought (Martín Benito et al. 2011, Will et al. 2015). Some of the studies attribute this pattern to the positive association between more fertile soils (i.e., higher soil N availability) and higher water holding capacity of the soil (i.e., due to higher organic matter content) that would buffer plants from the negative effects of growing during a drought event (Lévesque et al. 2016). This dichotomy of responses illustrates our lack of a thorough understanding on how multiple agents of global change may interact and affect future productivity of forest ecosystems.

To better understand how the effects of environmental conditions and anthropogenic N deposition may interact to influence tree growth, and thus forest productivity, we analyzed 20 years of radial growth increments from a dominant tree species in eastern North American forests, *Acer saccharum* Marsh. Tree growth data were collected as part of a long-term experiment in which anthropogenic N deposition was increased annually across a latitudinal gradient. Specifically, we asked: 1) what are the optimal temperature and soil water conditions for tree growth, and do these differ between N treatments? 2) Do the effects of the experimental N deposition on tree growth depend on the environmental conditions trees are growing under? 3) Will these effects change under the climate scenarios forecasted for the region? Answers to these questions will position us to better assess the implications for forests growing under the combined effects of multiple global change drivers.

Methods

Study sites and experimental design - To address our research questions, we capitalized on the tree growth data collected as part of a long-term N deposition experiment that was initiated in 1994 across the upper Great Lakes Region, USA (Burton et al. 1991). This study provides a way to identify the combined, but not confounded, effects of N and environmental conditions on tree growth. Four experimental sites, naturally regenerated forests, were distributed along a temperature gradient encompassing most of the latitudinal range of the Northern Hardwood forests in eastern North America (Table 1). Sites were similar in age, soil properties and forest composition; differences among sites arise from temperature and ambient N deposition levels (Table 1). At each site, six 30x30 m plots were delineated, and in 1994 half of the plots started receiving N additions similar to those observed at the time in some parts of Europe and eastern USA (Bredemeier et al. 1998, Fenn et al. 1998). Nitrogen additions of 30 kg NO_3^--N ha^{-1}yr^{-1} above ambient were applied in six even applications (5 kg ha^{-1}yr^{-1}) over the growing season as solid $NaNO_3$.

Tree Growth - At the beginning of the experiment, all individual trees with a diameter at breast height (dbh; 1.37 m) > 5 cm were identified and numbered in each plot. Thereafter, dbh was measured every year in the autumn following leaf fall using tapes. Painted marks were placed at 1.37 m above the soil surface on each tree, ensuring all annual measurements were made at the same location along the tree bole (dbh data are available online[1]). The species we used in our analysis was *Acer saccharum*, the dominant overstory tree in all study sites. This is a highly shade-tolerant and slow-growing species that mainly occurs on fertile, moist and well-drained soils and has been characterized as highly susceptible to water limitation (Host and Pregitzer 1991). Annual tree radial growth was estimated as the difference in dbh between two consecutive years, for individual *i* in year *t* annual growth was: $G_{i,t} = dbh_{i,t}-dbh_{i,t-1}$. To avoid mortality driven growth declines (Wyckoff and Clark 2002), we only included trees that were alive during the entire period; mortality largely occurred in the smaller size classes (5 to 10 cm dbh). We had records for a total of 1016 individuals collected over 20 years (1994-2013). Estimates that were zero or negative were discarded and were considered measurement errors. To ensure we were not biasing the analysis we confirmed that the number of discarded data points was similar among

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[1] http://forest.mtu.edu/research/michigangradient/data.htm

treatments and that they did not show strong relationships with the environmental data (see Appendix S1).

Environmental data - At the center of each plot, air temperature and soil matric potential were collected during the study period. Temperature was measured at 2 m above the ground using thermistors (Model ES-060-SW, Wescor Inc., Logan, UT, USA); measurements were taken every 30 minutes. Soil matric potential was recorded at a depth of 15 cm using gypsum soil moisture blocks (Model 5201, Soilmoisture Equipment Corporation, Goleta, Ca, USA). Soil moisture block resistance values (ohms, recorded every 30 minutes and averaged every three hours) were converted to matric potential (MPa) using relationships developed for each site from intact soil cores equilibrated with soil moisture plates (Burton et al. 2004). We included temperature and soil matric potential in our analysis because both variables determine the water status of the plants. Temperature regulates water demand through its control on vapor pressure deficit, whereas soil matric potential provides a measurement of plant available water (Lambers et al. 2008). Prior to our analyses, we extensively explored the data to select the periods of time for which environmental variables had the highest correlations with growth. Temperature and matric potential during the summer (June, July and August) had the strongest associations with growth; thus, in the analysis we used monthly averages from those months.

Analysis and Simulations - We estimated the effects of temperature and soil matric potential on tree radial growth using the approach developed by Canham and Thomas (2010). Here, we present an overview, detailed explanations are provided in Appendix S2. We used our 20 years of individual tree data to identify the maximum growth rate observed for each tree ($Gmax_i^{obs}$; average maximum growth rates differed between sites and treatments, Table 1), we then analyzed each year's growth ($G_{i,t}$) as a deviation from that individual maximum as being mediated by the effects (E) of the temperature and soil matric potential. Because growth in previous years can affect current year's growth (lag effects; Bishop et al. 2015, Peltier et al. 2016), we also included an effect associated with growth during each of the previous four years. Thus, our analyses begin in year five after the initiation of the experiment in 1994 and are carried through 2013. In preliminary analyses (not shown) we also considered other variables that could be affecting growth, e.g., growing season length and leaf are index (LAI). Because they did not improve the fit of the analysis, we opted for the most parsimonious model, shown below.

We considered the true maximum growth potential of each tree, $Gmax_i^{true}$, to be a latent variable estimated from the data ($Gmax_i^{obs}$; which varied between 0.05 and 1.4 cm), $Gmax_i^{true} \sim Normal(Gmax_i^{obs}, 1)$. Estimating maximum growth rate for each individual tree allowed us to reflect individual variability in growth rates due to tree size, site characteristics and any other individual differences not considered (e.g., competitive environment, genetic differences). Annual growth data, *G*, were then analyzed as a function of this true estimate, *Gmax^true*, and the effects of temperature, soil moisture and previous years' growth, with likelihood:

$$G_{i,t} \sim Normal(Gm_{i,t}, \sigma_{treatment(i)}^2)$$

and process model:

$$Gm_{i,t} = Gmax_i^{True} \cdot TemperatureE_{i,t,treatment(i)}$$
$$\cdot \text{Soil } MoistureE_{i,t,treatment(i)} \cdot PreviousGrowthE_{i,t,treatment(i)}$$

Under optimal conditions, effects are equal to one ($E = 1$) and trees would reach their maximum growth rate (*Gmax_i*). If conditions deviate from their optima, then the effects decreased following a Gaussian curve (E<1) and the individual tree would not reach its maximum growth rate (see Appendix S2 for detailed description of how the effects were estimated).

Because growth in a particular year can be affected by environmental conditions taking place in previous years (Bauce and Allen 1991, Bishop et al. 2015), the effect of temperature and soil moisture, *TemperatureE* and *SoilMoistureE*, were estimated for the current year, as well as a function of the previous two years of environmental data. To assess which month and which year of environmental data was most influential we weighed the contribution of each summer month and year following Ogle et al. (2015) (see Appendix S3 for detailed description about the estimation of the weights). The influence of each of the four previous years of growth, *PreviousGrowthE*, on current year's growth, $G_{i,t}$, was also weighed using the same method (Appendix S3). We assessed the effects of the N deposition treatment on growth by estimating effect sizes (ES: ln[N deposition/ambient]) of the combined temperature and soil moisture effects ($G_{max} \cdot TemperatureE \cdot SoilMoistureE$).

In addition, using parameter estimates, posterior means, variances and covariances, we simulated growth rates for each tree under two climate scenarios developed specifically for the region (as part of a Forest Vulnerability Assessment, Handler et al. 2014). The first scenario (S1)

accounts for moderate changes (0.7°C temperature rise and 14.28% precipitation increase in the summer), driven by a decline in CO_2 emissions (PCMB1). The second, more-extreme scenario (S2; 5.7°C temperature increase and 40% precipitation decrease in the summer) is based on current emissions that are maintained into the future (GFDLA1F1). Simulations were run on the same tree data, starting in year one of the analysis, for the same number of years we analyzed. We modified the recorded environmental data according to the projections from the climate scenarios (increasing temperature [°C] and increasing or decreasing soil water [MPa], for latest estimates we used the same relationships developed for each site [Burton et. al. 2004]); thus, simulations incorporate the year-to-year variability documented in the data. We then compared average site and treatment growth estimates with those in the data (*i.e.,* current conditions).

All model parameters were estimated following a Bayesian approach from non-informative distributions (Appendix S4). Model runs were carried out in OpenBUGS (Thomas et al. 2006; see Appendix S5 for model code). We ran three different chains for 30,000 iterations. Parameter values and effect sizes were estimated after convergence of the chains.

Results

For the final analysis, we had a total of 11,081 estimates of tree growth; which varied substantially over the 20-year period used in our analyses (see Appendix S6 for graphical summaries of the data). Further, air temperature and soil matric potential exhibited considerable variability among sites and across years (Appendix S6). The fit of the radial growth submodel (G, R^2 for predicted *vs* observed radial growth) was 0.54, and for the maximum growth submodel (*Gmax*) it was 0.87. All model parameters are reported in Appendix S7.

Effects of temperature and soil water - The temperature and soil matric potential for optimal growth were similar for the ambient and experimental N deposition treatments (Fig. 1). Growth rates peaked at ~16°C temperature (mean±SD: 16.3±0.12 ambient and 15.8±0.28 N deposition, these are the combined estimates of June-July-August averages during current and previous two years), a slightly cooler temperature than the average in the data (~17°C), and at a matric potential of -0.45 MPa (mean±SD: -0.45±0.05 ambient and -0.46±0.06 N deposition), also a slightly lower value than the data average (-0.35 MPa). However, growth estimates differed between treatments and these differences increased as conditions departed from the optima (95% predicted growth intervals do not overlap; Fig. 1), with growth decline being slower under experimental N deposition. The variances for the temperature effect for ambient and N

deposition were 7.98±1.06 and 15.03±3.58 respectively, for the soil moisture effect were 0.32±0.1 ambient and 0.48±0.17 N deposition. Weight estimates indicate that the temperature regime taking place during the previous year (*t-1*), and, in particular, temperature during the month of June (in every year), were most influential on current-year tree grow (see Appendix S7 for estimates). The soil matric potential values that most influenced growth were those taken place two years previous to current (*t-2*), specifically during the month of August (Appendix S7).

Effects of previous years' growth - The effect of previous years' growth on current year growth was similar between treatments and peaked beyond the range of your data (Fig. 1; optima at 2.28±0.29 cm yr^{-1} for ambient and 3.31±0.4 cm yr^{-1} for N deposition, and variances 4.01±1.18 in ambient and 8.08±2.15 in N deposition). The most influential lag effects of past growth on current year were those from three years before (*t-3*, Appendix S7).

Effect of N deposition treatment under varying environmental conditions - In general, tree growth rates were always higher under the N deposition treatment (positive and statistically significant ES values in Fig. 2). And, as conditions deviated from optimal temperature or soil moisture, the differences between the two treatments escalated, being greatest under the most negative matric potentials; this was accentuated by increasing temperatures (Fig. 2).

Changes in the effects of N deposition treatment under the forecasted climate - Predictions of average radial growth for each site and N deposition treatment under current and forecasted conditions reveal growth rates consistently higher under experimental N deposition, and in most cases this difference was significant (Fig. 3 comparisons between black and red symbols). As predictions move through the climatic scenarios, growth would be slightly negatively affected under S1, especially in the warmer southern sites. Comparisons with the S2 predictions reveal a large and consistently significant decrease in growth across sites and treatments (Fig. 3 comparisons within symbols of the same color).

Discussion

To better understand the concurrent effect of changing environmental conditions and future rates of anthropogenic N deposition on tree growth, we analyzed two decades of growth data from a dominant tree species in eastern North American forests. The environmental variability of the data, both spatially and temporally, as well as the design of our replicated experiment across a region, allowed us to quantify the long-term effects of anthropogenic N deposition on tree growth under a wide array of growing conditions. Here, we demonstrate adult tree growth rates

are always higher, and mostly significantly so, under experimental N deposition. Furthermore, our analysis revealed that the optimal conditions for tree growth were similar between ambient and experimental N deposition. However, as temperature increased and soil matric potential declined, tree growth decreased from its maximum potential at a slower pace under experimental N deposition. Growth predicted under the forecasted climatic scenarios revealed a strong decline under the most extreme forecast. Thus, even if elevated N deposition has an ameliorating effect under less favorable environmental conditions, the decrease in tree growth due to climate change will not be fully lessened by growing under anthropogenic N deposition levels.

1) What are the optimal temperature and soil water conditions for tree growth, and do these differ between N treatments? Numerous tree species are adapted to grow under a wide range of environmental conditions, which is reflected in their large distributional ranges (Little 1971). However, their functional performance does vary along climatic gradients and determines their competitive ability at any given site (Marcora et al. 2008, García et al. 2000). Understanding these differences, and quantifying how growth and fecundity may deviate from their optima, becomes critical for forecasting future performance under changing conditions (Valladares et al. 2014). The temporal and spatial extent of our study enabled us to estimate the optimal climatic conditions under which growth of *A. saccharum* was maximized in this region. Optimal temperature and soil water availability were similar under ambient and experimental N deposition. Importantly, what differed between treatments was the departure from their optimal conditions (Fig. 1).

Negative growth responses to warmer temperatures and drier soils have been previously documented in *A. saccharum* (e.g., Gavin et al. 2008, Bishop et al. 2015). Temperature has a myriad of effects on the physiological processes that underlie plant growth (e.g., affects respiration, photosynthesis, transpiration, storage). Among these, one of the most relevant effects for plant performance is related to how temperature regulates water demand given the strong relationship between temperature and vapor pressure deficit, which increases exponentially with temperature (Lambers et al. 2008). Thus, under warmer conditions plants experience a higher demand for water that may not be met, causing stomatal closure and reduced photosynthetic assimilation (Bahari et al. 1985). Overall, our results indicate that as water demand increases under warmer conditions, soil water, even if it remains the same, might not be sufficient to sustain growth. This agrees with previous work on this drought intolerant species, in which

reductions in photosynthetic and growth performance have been linked to soil water limitation (Peltier and Ibáñez 2015, Gunderson et al. 2000, Walters and Reich 1997). In addtion, the fact that previous years' performance also had an effect on growth illustrates how the effect of adverse conditions in one particular year could have repercussions on plant performance over subsequent years (Peltier et al. 2016).

2) Do the effects of the N addition treatment on tree growth vary as a function of the environmental conditions trees are growing under? Field studies analyzing tree growth in response to drought have also reported higher resilience to drought under higher levels of soil N availability (Lévesque et al. 2016). However, these beneficial effects were attributed to the greater water holding capacity of fertile soils, due to their higher organic matter content (Baribault et al. 2010). With our experimental design, we were able to separate the effect of growing under ambient and experimental N deposition from those imposed by temperature and soil water availability. During our 20-year study period, at each site, soil water potential did not differ between N deposition treatments (see Appendix S8 for data and analysis); thus, the beneficial effect of anthropogenic N deposition on tree growth is not related to any difference in soil water availability between treatments. Leaf production, measured as LAI (Table 1), was slightly higher, but not significantly so, under experimental N deposition; therefore, it is unlikely that these small ecological differences would account for their higher growth rates, especially during adverse environmental conditions. Maggard et al. (2016) observed that fertilization of *Pinus taeda* reduced stomatal conductance, but not photosynthesis; if this were to be the case with our study species, it would explain the larger differences in growth performance under dry soil conditions. However, Talhalem et al. (2011) did not observed differences in photosynthesis between treatments at one of our sites. Another mechanism plausibly explaining our results could be related to tree conduit architecture. A meta-analysis assessing the effect of anthropogenic N deposition on growth of several tree species in Europe (including an *Acer*) found that N availability might facilitate the construction of a xylem structure (more conduits per unit area) that is more efficient for water transport under wet conditions and more resilient to embolism under drought conditions (Borghetti et al. 2016). Such response could account for higher growth rates under experimental N deposition in both wet and dry conditions, but this would need to be confirmed by direct observation of tree wood anatomy. Also, higher nutrient availability during

drought has been associated with higher water use efficiency and lower risk of carbon starvation (Gessler et al. 2017), and thus, higher growth.

Our analyses revealed that growth differences between N deposition treatments were accentuated under more adverse conditions of temperature and soil water availability (Fig. 2). Several field studies have documented that the enhancement of tree growth by anthropogenic N deposition may be ameliorated when plants are growing under suboptimal environmental conditions (Magnani et al. 2007, Bedison and McNeil 2009). However, in these studies, it is not entirely possible to separate the effects of anthropogenic N deposition from other factors that also influence tree growth. The unique characteristics of our experimental design, data from trees growing under the same environmental conditions under ambient and experimental N deposition, allowed us to isolate the effects of anthropogenic N deposition from other limiting factors.

3) Will the effect of growing under N addition treatment change under the predicted climate scenarios for the region? When we predicted growth rates under current and forecasted scenarios, we were able to assess the magnitude of the N deposition treatment on growth. Predictions under S1, moderate scenario, differ little from those recorded in the data (Fig. 3). However, under the S2 scenario growth rates could decrease by three-fold among sites and treatments (Fig. 3; decreases ranged between 2.73 and 3.98 times). Still, the positive effect of anthropogenic N deposition on tree growth appears to be sustained even under this most extreme scenario (Fig. 3). For example, effect sizes among sites averaged (mean±SD) 0.12±0.07 under current conditions and they increased to 0.34±0.03 under the S2 scenario; thus, the growth-enhancing effect of experimental N deposition appears to continue under adverse conditions. Our results contradict findings from seedling and sapling experiments, in which the plants most affected by water limitation were those growing under conditions of high soil N availability (Nagakura et al. 2008, Vandereeden et al. 1992). These discrepancies are likely due to the ontogenetic stages considered; that is, the growth response of young seedlings to that of mature adult trees. In a previous analysis of the same data (Ibáñez et al. 2016), we documented both higher mortality and higher relative growth rate among the smallest tree size classes under experimental N deposition. Although not implicit in that analysis, these trends would agree with the reported negative effects of experimental N deposition under adverse conditions when considering early ontogenetic stages. Younger trees, ~5 cm dbh, grew faster under experimental N deposition and that excess growth could have become detrimental during adverse conditions

(i.e., higher maintenance costs to support a greater biomass under the forest canopy), resulting in higher mortality in dry years (Rose et al. 2009, Kobe 2006), while mature trees could have accessed deeper water sources due to a more extensive root system. Therefore, any assessment of the combined effects of anthropogenic N deposition and water limitation should consider potential variability of responses across ontogenetic stages of tree development.

Conclusions

Forest tree species are simultaneously exposed to the influence of several interactive aspects of global change, understanding their integrated effects on tree growth becomes essential to reliably predict forest functioning into the future (Loehle et al. 2016, Hungate et al. 2003). In our experiment, we were able to separate the effects of anthropogenic N deposition on tree growth from those associated with temperature and water limitation, which enabled us to assess how the effects of temperature and soil water availability varied with N deposition treatment as well as how N deposition may affect tree growth under the forecasted climate scenarios for the region. In addition, our results shed light into the contradictory growth responses reported in other studies, in which anthropogenic N deposition has elicited both beneficial (natural field gradients) and detrimental (controlled seedling and sapling experiments) effects on trees. Our results indicate that, at least for adult tree stages, growing under anthropogenic N deposition may ameliorate some of the negative effects of water limitation. However, despite the positive effect of N deposition on radial growth, and the increase of this effect under more adverse conditions, anthropogenic N deposition will not fully compensate for the negative effects of growing under the forecasted climate. Thus, we should expect a decrease in *A. saccharum* growth across the geographic range of our study, in which water demand may increase and soil water may become a limiting resource as the Earth's climate continues to change into the future.

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Table 1. Mean (±SD) climatic, edaphic and ecological characteristics of four study sites distributed across a climate gradient across Michigan's Upper and Lower Peninsulas. BA: basal area, LAI: leaf area index.

Site variables	Site A	Site B	Site C	Site D

	(most northern)	(northern)	(southern)	(most southern)
Location	46°52'N	45°33'N	44°23'N	43°40'N
	88°53'W	84°52'W	85°50'W	86°09'W
Temperature	4.8°C	6.1°C	6.9°C	7.6°C
Precipitation	821 mm	828 mm	856 mm	793 mm
†Ozone	88±14.1 ppb		80.41±7.73 ppb	
Age	107 yr	101 yr	102 yr	105 yr
*Soil sand	85%	89%	89%	87%
*Soil pH	4.83	5.03	4.47	4.66
*Soil organic C	19.0 mg C/g	19.4 mg C/g	15.4 mg C/g	18.4 mg C/g
**Soil Ca^{++}	31 g/m^2	140 g/m^2	45 g/m^2	53 g/m^2
*N deposition	0.68 g $m^{-2}yr^{-1}$	0.91 g $m^{-2}yr^{-1}$	1.17 g $m^{-2}yr^{-1}$	1.18 g $m^{-2}yr^{-1}$
Acer BA	32.6 cm^2m^{-2}	29.4 cm^2m^{-2}	26.5 cm^2m^{-2}	25.1 cm^2m^{-2}
Total BA	36.6 cm^2m^{-2}	33.9 cm^2m^{-2}	34.8 cm^2m^{-2}	39.1 cm^2m^{-2}
***$LAI_{ambient}$	5.96±0.58	6.67±1.28	7.59±1	7.8±0.78
***$LAI_{N\ deposition}$	6.17±0.58	7.08±1.28	7.24±0.84	8.26±0.09
$Gmax_{ambient}$	0.32±0.19 cm	0.34±0.16 cm	0.31±0.17 cm	0.33±0.20 cm
$Gmax_{N\ deposition}$	0.36±0.20 cm	0.40±0.20 cm	0.40±0.25 cm	0.36±0.18 cm

†Ozone levels are based on the highest 8 hr of ozone concentrations recorded at the two monitoring stations closest to the sites, Seney (sites A and B), and Houghton Lake (sites C and D). Values were available for the period 2002-2013.

*Values at the beginning of the experiment, 1993 (Burton et al. 1991).

**Exchangeable Ca. Base saturation in surface soils ranged from 70 to 96%.

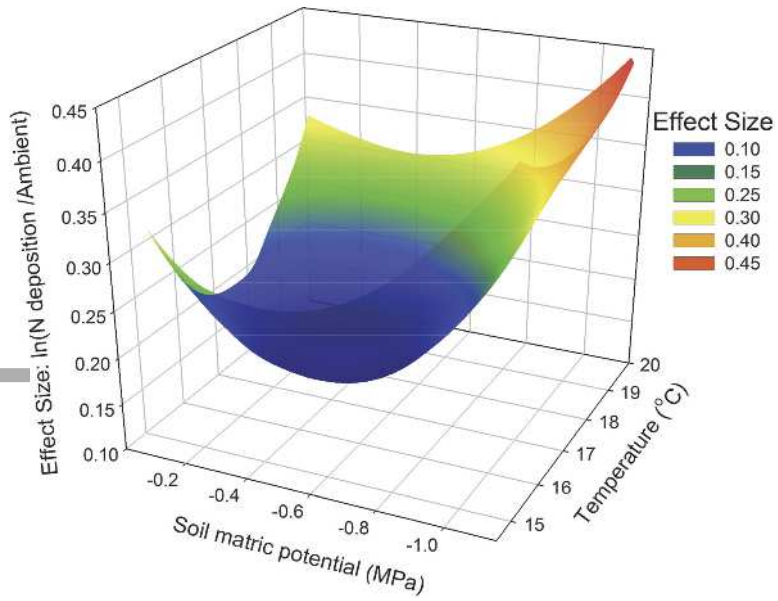***LAI data was estimated from litter trap collections, see Burton et al. 1991.

Figure 1. Effect of temperature, soil moisture and previous years' growth on tree radial growth, shown as: $G_{max} \cdot Effect$ (G_{max} values were average across sites for each N deposition treatment). Circles represent growth data associated with the effect of each variable; curves indicate the average response. Vertical dashed lines show the values of temperature and soil moisture at which optimal growth is reached.

Figure 2. Effect size of the combined effects of temperature and soil moisture on growth (expressed as ES:ln[Growth Ndeposition/Growth Ambient]; Growth: $G_{max} \cdot TemperatureE \cdot SoilMoistureE$, for this calculation G_{max} was average across sites for each N deposition treatment). For clarity only average values are plotted, all ES values were positive and statistically significant, the 95%CI did not include zero.
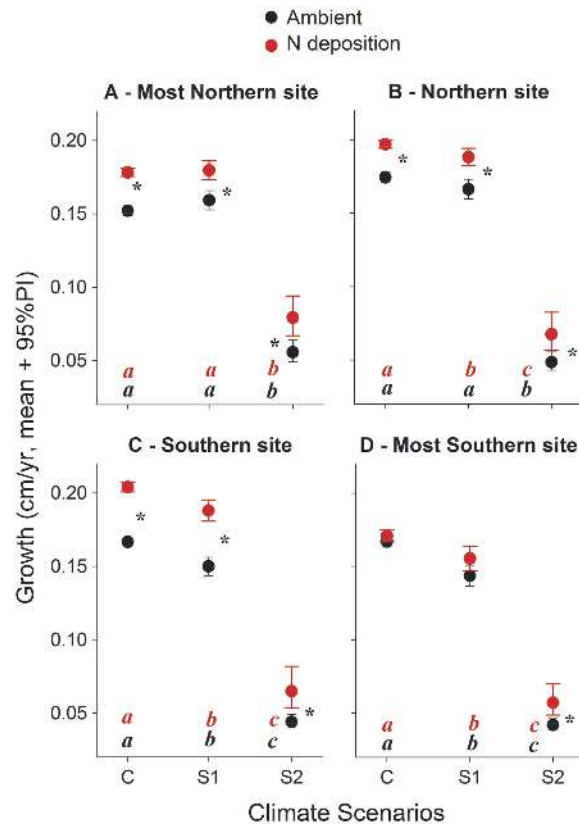
Figure 3. Average growth estimates (means+95% predicted interval) for each site and treatment combination under current environmental conditions (C, based on collected environmental data during the study period) and under the two climate scenarios forecasted for the region, S1 (moderate changes) and S2 (more extreme changes). Asterisks indicate N treatments are significantly different, 95% PI do not overlap; within each treatment, i.e., same color, different letters between climatic scenarios reflect statistically significant differences.

Effect of Temperature

Effect of Soil moisture

Effect of previous Growth
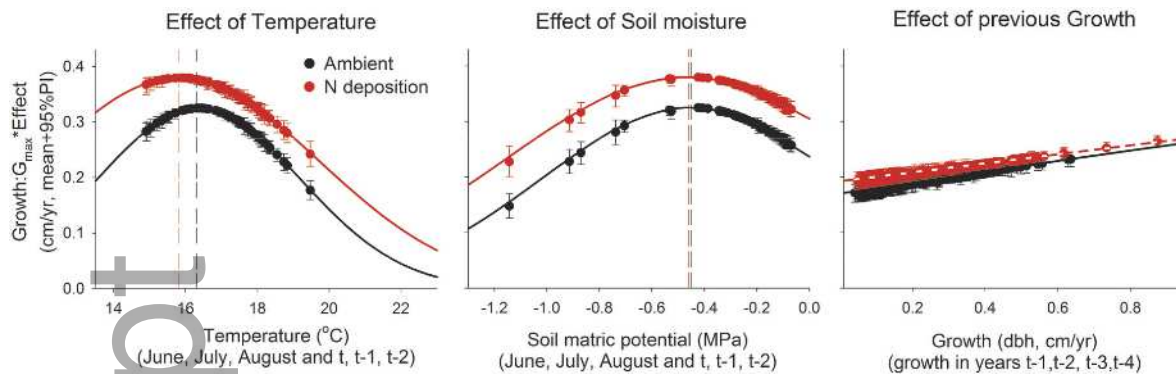
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