Ecology, 96(6), 2015, pp. 1459–1465

Anthropogenic nitrogen deposition predicts local grassland primary production worldwide

Carly J. Stevens,[1,21] Eric M. Lind,[2] Yann Hautier,[2,3] W. Stanley Harpole,[4,5,6,7] Elizabeth T. Borer,[2]
Sarah Hobbie,[2] Eric W. Seabloom,[2] Laura Ladwig,[8] Jonathan D. Bakker,[9] Chengjin Chu,[10] Scott Collins,[8]
Kendi F. Davies,[11] Jennifer Firn,[12] Helmut Hillebrand,[13] Kimberly J. La Pierre,[14] Andrew MacDougall,[15]
Brett Melbourne,[11] Rebecca L. McCulley,[16] John Morgan,[17] John L. Orrock,[18] Suzanne M. Prober,[19]
Anita C. Risch,[20] Martin Schuetz,[20] and Peter D. Wragg[2]

[1]*Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ United Kingdom*
[2]*Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108 USA*
[3]*Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB United Kingdom*
[4]*Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, Iowa 50011 USA*
[5]*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig, Germany*
[6]*Department of Physiological Diversity, Helmholtz Center for Environmental Research–UFZ, Permoserstrasse 15, 04318 Leipzig, Germany*
[7]*Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany*
[8]*Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA*
[9]*School of Environmental and Forest Sciences, University of Washington, Box 354115, Seattle, Washington 98195-4115 USA*
[10]*State Key Laboratory of Grassland and Agro-Ecosystems, Research Station of Alpine Meadow and Wetland Ecosystems, School of Life Sciences, Lanzhou University, Lanzhou 730000 China*
[11]*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA*
[12]*School of Earth, Environmental and Biological Sciences, Queensland University of Technology, Brisbane, Queensland 4001 Australia*
[13]*Institute for Chemistry and Biology of the Marine Environment, Carl-von Ossietzky University Oldenburg, Germany*
[14]*Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06511 USA*
[15]*Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1 Canada*
[16]*Department of Plant and Soil Sciences, University of Kentucky, Lexington, Kentucky 40546-0091 USA*
[17]*Department of Botany, La Trobe University, Bundoora, Victoria 3086 Australia*
[18]*Department of Zoology, University of Wisconsin, Madison, Wisconsin 53704 USA*
[19]*CSIRO Land and Water Flagship and the Great Western Woodlands Supersite, Private Bag 5, Wembley, Western Australia 6913 Australia*
[20]*Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf 8903 Switzerland*

Abstract. Humans dominate many important Earth system processes including the nitrogen (N) cycle. Atmospheric N deposition affects fundamental processes such as carbon cycling, climate regulation, and biodiversity, and could result in changes to fundamental Earth system processes such as primary production. Both modelling and experimentation have suggested a role for anthropogenically altered N deposition in increasing productivity, nevertheless, current understanding of the relative strength of N deposition with respect to other controls on production such as edaphic conditions and climate is limited. Here we use an international multiscale data set to show that atmospheric N deposition is positively correlated to aboveground net primary production (ANPP) observed at the 1-m^2 level across a wide range of herbaceous ecosystems. N deposition was a better predictor than climatic drivers and local soil conditions, explaining 16% of observed variation in ANPP globally with an increase of 1 kg N·ha^{-1}·yr^{-1} increasing ANPP by 3%. Soil pH explained 8% of observed variation in ANPP while climatic drivers showed no significant relationship. Our results illustrate that the incorporation of global N deposition patterns in Earth system models are likely to substantially improve estimates of primary production in herbaceous systems. In herbaceous systems across the world, humans appear to be partially driving local ANPP through impacts on the N cycle.

Key words: Anthropocene; Bayesian analysis; hierarchical regression; nitrogen deposition; Nutrient Network; primary production.

INTRODUCTION

The global anthropogenic creation of reactive N has increased from approximately 15 Tg N in 1860 to 187 Tg N in 2005, largely driven by a global demand for food and increase in energy production (Galloway et al. 2004). This unprecedented anthropogenic impact on the

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Manuscript received 6 October 2014; revised 30 January 2015; accepted 4 February 2015. Corresponding Editor: J. B. Yavitt.

[21] E-mail: c.stevens@lancaster.ac.uk

global N cycle has exceeded recommended boundaries that ensure resilience of Earth system functioning (Rockström et al. 2009). This reactive N enters the N cycle through agricultural and industrial activity, eventually resulting in increased atmospheric N deposition, which can alter fundamental processes such as carbon cycling, climate regulation, and biodiversity (Sutton et al. 2011). This anthropogenically created N also leads to changes in biogeochemical cycles; in particular, availability of mobile forms of N in the soil are increased, rates of N turnover through processes such as decomposition, mineralization, and nitrification are altered, N is lost to downstream systems via leaching, and ammonia volatilization and denitrification are increased (Sutton et al. 2011). N deposition can acidify soils leading to further impacts on biogeochemical cycling such as changes in the availability of metals (Tyler and Olsson 2001) and in enzyme activity (Sinsabaugh et al. 2008). Furthermore, atmospheric N deposition can have serious, negative consequences for biodiversity (Stevens et al. 2004, Clark and Tilman 2008).

Theoretical and empirical models (Vitousek and Howarth 1991) have emphasized that plant production should be limited in part by the supply of biologically available N. Local experiments in herbaceous systems confirm that in many cases primary productivity increases in response to N addition (e.g., Fenn et al. 2003, Clark and Tilman 2008, Hautier et al. 2009, Phoenix et al. 2012). In forest ecosystems, N deposition is thought to be a major driver of carbon sequestration in part through increased tree growth rates (Thomas et al. 2010). However, in contrast to herbaceous systems, tree death has been associated with N deposition due to nutrient imbalances, loss of mycorrhizal associations and interaction with secondary stressors (Aber 1992, Erisman and De Vries 2000). Whether or not these same feedbacks occur, there is considerable potential for changes in ANPP in grassland ecosystems impacted by anthropogenic N since primary production in most grasslands is limited in part by the supply of biologically available N (Vitousek and Howarth 1991).

Earth systems models generally account for effects of regional temperature and precipitation, atmospheric CO_2, photosynthetically active radiation, and vegetation type to estimate global patterns of ANPP (Lauenroth 1986). Given the considerable perturbation of the global N cycle, it is likely that N deposition is impacting global ANPP, but only recently have these dynamics been considered explicitly with respect to global carbon cycles (Zaehle 2013), and uncertainty remains on the relative influence of this reactive N on productivity. For instance, three of the global carbon cycle models in the most recent Intergovernmental Panel on Climate Change report include reactive N dynamics (including N deposition), but seven others do not (Ciais et al. 2013). The link between primary production and atmospheric N is further obscured because of a fundamental mismatch of scales between measurements and drivers of ANPP. ANPP can be influenced by local edaphic conditions as well as by large-scale climatic forces, greatly complicating clear inference. Meta-analyses have linked terrestrial NPP and experimental N manipulation have demonstrated increases in NPP with increasing N addition (LeBauer and Treseder 2008, Lee et al. 2010). As such, although primary production is inherently linked to the carrying capacity of the biosphere, and anthropogenic N deposition has the potential to influence global ANPP, it is not well known how ambient N deposition drives terrestrial ANPP at a global scale and whether the influence of atmospheric N, if it exists, rivals the influence of well-known drivers of ANPP such as temperature and precipitation, or local soil properties. Although understanding the forces that drive biological productivity of herbaceous systems are critically important, and global models have indicated a strong role for N deposition (Zaehle 2013), these relationships have not been empirically evaluated because we generally lack globally distributed data sets collected at the local scale using consistent protocols.

To address this knowledge gap, we combined a coherent global model of atmospheric N deposition, long-term, site-level, climatic data, and fine-scale (1-m^2) productivity estimates taken in herbaceous systems worldwide. Specifically we asked, does atmospheric N deposition predict locally observed grassland production? And if so, how does the strength of this N deposition effect compare to other known drivers of production such as climatic variables at the site level, and edaphic conditions at the plot level?

METHODS

Data collection

We used biomass production data from 42 sites on four continents (Fig. 1), which are members of the Nutrient Network Global Research Cooperative (Appendix B: Table B1). Each site is dominated by low-statured, primarily herbaceous vegetation located in a patch of at least 1000 m^2 of relatively homogeneous vegetation while representing the heterogeneity characteristic of the given site. Vegetation is representative of each region, comprising a very broad range of herbaceous communities including annual and perennial grasslands, prairies, alpine meadows, old fields, savannas, and salt marshes. At each site, 5×5 m plots were established (mode 30, range 8–60 plots). Growing season peak standing crop was estimated destructively by clipping all aboveground biomass of plants rooted within two 0.1×1 m strips within each plot. Thirty sites were harvested in 2007, seven sites in 2008, three sites in 2009, and two sites in 2010. Biomass was sorted into current (live and recently senescent material) and previous years' growth to give aboveground net primary production (ANPP; Lauenroth et al. 2006) and total biomass (all clipped material). For shrubs and subshrubs (dwarf shrubs), all leaves and current year's

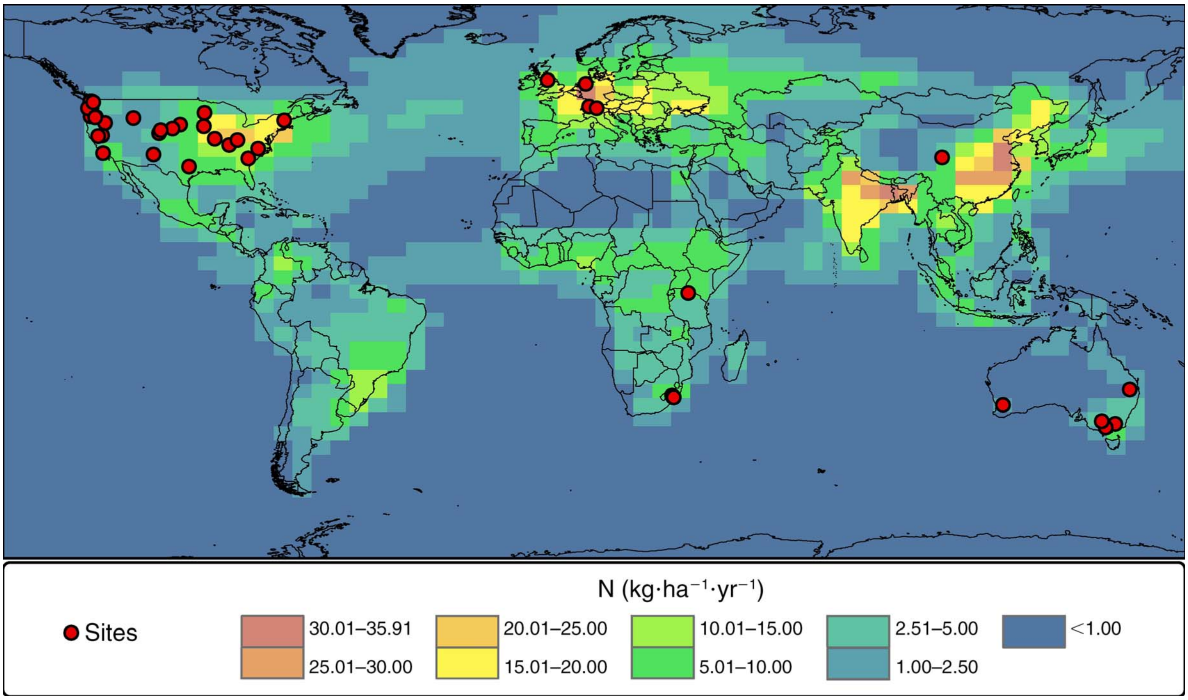

FIG. 1. Map of modeled N deposition rates at sites used in study. Circles indicate the Nutrient Network sites used in the analysis. Further details of sites are given in Appendix B: Table B1.

stems were collected. All biomass was dried at 60°C for 48 hours, and weighed to the nearest 0.01 g. From the cleared biomass strip, a soil sample was taken (three 2.5 cm diameter cores to 10 cm depth, approximately 150 g), dried to constant mass and analyzed for pH, percent total C, percent total N, and P (ppm). Full details of Nutrient Network methods can be found in Borer et al. (2014).

Site location (latitude and longitude) was used to determine total atmospheric N deposition (kg N·ha^{-1}·yr^{-1}) based on modeled output of Dentener (2006) for the year 1993. The modeled output uses a global three-dimensional chemistry-transport model, emissions estimates and projected climate scenario data (Dentener 2006). The model has a cell size of 5° longitude (~555 km at the equator) by 3.75° latitude (~407 km). The large cell size and mismatch between the sampling year and N deposition estimates limits the accuracy of the model application to a single site, as does the discrepancy between the year of the model and the year of data collection but the data set remains the most coherent, directly comparable global data set for analysis of N deposition patterns.

Estimates of climatic covariates known or thought to influence plant production were also obtained. Mean annual precipitation (MAP, mm) and mean annual temperature (MAT, °C) were derived from WorldClim (Hijmans et al. 2005) and annual potential evapotranspiration (PET, mm) was taken from the CGIAR-CSI Global PET database (Zomer et al. 2008) based on site location.

Data analysis

Effects of climate, elevation, edaphic conditions, and atmospheric N deposition on ANPP were estimated using multilevel regression modeling in a hierarchical Bayesian framework. This framework, unlike traditional variance components analysis or mixed-effects models, allows direct comparisons of effect sizes across scales (e.g., plot- vs. site-level predictors; Hector et al. 2011). Due to high collinearity (Pearson $r = 0.85$) between MAT and PET we used only PET in the final model; a similar model with a principal components axis capturing >90% of the variation in MAT and PET yielded equivalent results. Explanatory variables were normalized (scaled and centered around 0) to allow for meaningful comparisons of effect sizes (coefficients of variation for each predictor are provided in Appendix B: Table B2). Plot-level variables (soil nutrients and pH) were modeled as linear predictors of ANPP (log-transformed live biomass) at the plot level. Site-level variables (MAP, PET, elevation, and N deposition) were modeled as predictors of the site intercept (expected mean ANPP) and predictors of the slopes of the plot level edaphic predictors. Thus the slope of the relationship between each soil variable and ANPP could differ by site, and could interact with site-level predictors. The slopes of plot-level predictors were also allowed to covary within sites, and the strength of this covariance was quantified across all sites. We implement-

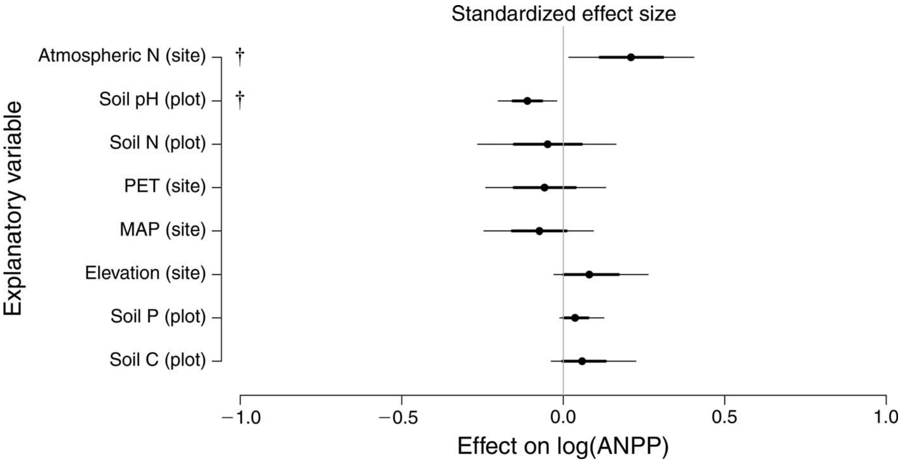

FIG. 2. Standardized effect size estimates of multiscale predictors of aboveground net primary production (ANPP). Shown are probability distributions of effect of predictors on observed production (on log-linear scale) drawn from posterior distribution of multilevel model. Points are mean standardized effect estimate, thick bars are 68% credible intervals, thin bars are 95% credible intervals. Predictors with 95% credible intervals that do not include zero are considered significant effects and denoted by daggers (†). Abbreviations are PET, potential evapotranspiration; MAP, mean annual precipitation.

ed this model using JAGS and the R2jags package in R v3.0.2 (R Development Core Team 2013), running three independent Markov chain Monte Carlo (MCMC) simulations of 100 000 steps, discarding the first 5000 iterations and sampling 1 in 200 of the remaining realizations of the posterior probabilities. This gave a combined total of 1425 samples from the posterior distribution. Convergence in parameter estimation was confirmed by visually examining trace plots of chain iterations, and by ensuring Gelman-Rubin statistic values were less than 1.1. Posterior prediction model error checking and a Bayesian P value close to 0.5 also indicated appropriate model fit (Appendix B: Fig. B1). Significance of predictor slopes was determined by 95% posterior credible intervals that did not include zero. Further details of the modeling process are available online in Appendix A.

RESULTS

Climatic variables like PET and MAP are typically used as predictors of ANPP (Lauenroth 1986) but we found that the N deposition provides predictive power approximately twice as effective as the strongest conventional climate predictors, and strikingly, N deposition as estimated in the global model has stronger mean explanatory power of fine-scale primary production than any of the plot-level edaphic conditions (Fig. 2). Grassland ANPP was associated with increasing N deposition, and with decreasing soil pH, across the global data set (Figs. 2 and 3). Each additional unit of N deposition (kg $N \cdot ha^{-1} \cdot yr^{-1}$) corresponded to a roughly 3% increase in ANPP (Fig. 3a). While N deposition rate was negatively correlated with PET ($r = -0.32$, $P = 0.04$ on scaled and centered data), and positively correlated with MAP ($r = 0.33$, $P = 0.03$), models without N deposition did not recover PET or MAP as global predictors of ANPP and had a significantly worse fit than those including N deposition (Appendix B: Fig. B1). Removing the highest N deposition site (Germany) did not result in a loss of this relationship (Fig. B2). On the SD scale (the square roots of the variance components, to allow comparison of effects across levels (Hector et al. 2011), N deposition explained 16% of variation in ANPP, suggesting that N deposition has become an important driver of global herbaceous production (Schulze 1989). The relationship between ANPP and N deposition did not appear to saturate or switch to become negative at high levels of N deposition. A further 8% of variation in ANPP was explained by soil pH across all observations, though within-site relationships differed widely (Fig. 3b). Soil pH can be reduced by N deposition but is also driven by a range of other factors including underlying geology. However, there were no statistical interactions between the N deposition and pH effects, meaning within-site pH influence on production did not change predictably with N deposition level (Fig. B3). Other predictors explained similar levels of variation (MAP, elevation, and PET each 7%; soil C 7%; and soil P and N each 5%).

Regional analysis shows that although MAP was not a universal predictor of productivity, it was a good predictor of productivity variation in some regions (Appendix B: Fig. B5). In contrast, the clear effect of N deposition on ANPP was positive across sites within region as well as globally (Fig. B5).

DISCUSSION

The lack of relationship between ANPP and rainfall (MAP) or evapotranspiration (PET) with ANPP seems at first to contradict well-known relationships (Lauenroth et al. 2006). Upon inspection, MAP is a good predictor of productivity variation in some regions,

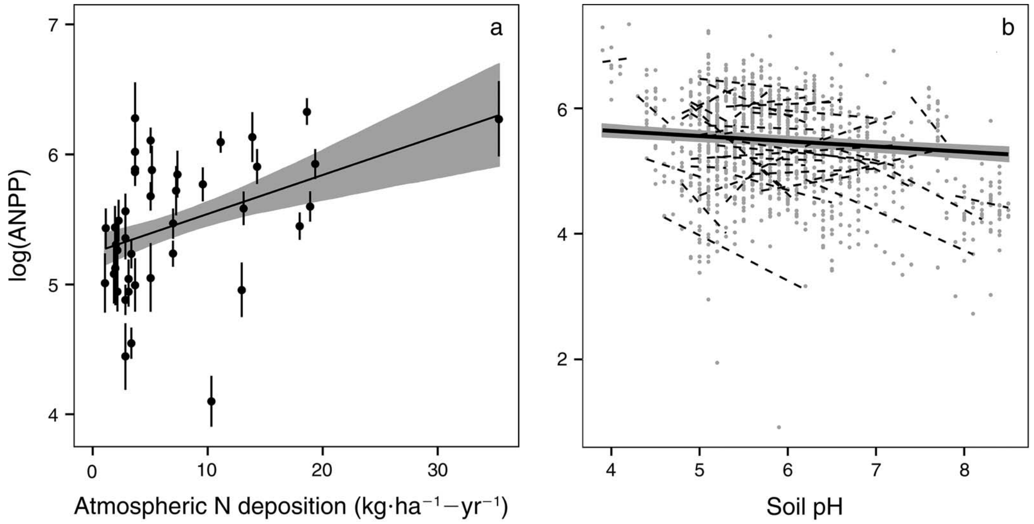

FIG. 3. Bivariate relationships of significant predictors. Aboveground live biomass (ANPP, measured as g/m^2), shown in relation to (a) site-level atmospheric N deposition and (b) plot-level soil pH. In (a), points are modeled site mean intercept values ± SE; in (b), points are observed plot-level production. Solid lines are slopes of effects estimated from a multilevel model, estimated at the mean of other site-level predictors (e.g., N deposition effect is shown for sites at global mean MAP and PET). Dashed lines in (b) are within-site trend lines. Shaded regions depict ±SE of the slope estimates.

namely the grasslands of central North America and Australia (Appendix B: Fig. B5). However these data span multiple regions and influences of climatic variables can differ strongly by region, making it difficult to discern in global analyses (O'Halloran et al. 2013). Although this data is from a limited number of sites and some sites are geographically clustered they span a broad range of climatic conditions (mean annual temperature 0.3°–22.1°C; Mean annual precipitation 252–2072 mm; Table B1) so it seems likely that relationships observed reflect global patterns. In dry regions, the effect of N deposition may only be apparent in wetter years; thus it is likely that our statistical model under-predicts the response in wet years but over-predicts it in dry years. Under a changing climatic regime this climatic variation may impact on effects of N deposition in some parts of the world. The climatic variability reinforces the importance of our finding of the general role of N deposition on ecosystem production across herbaceous-dominated ecosystems worldwide.

In contrast to the regional contingency in precipitation effects, the effect of N deposition on grassland ANPP was positive across sites within region as well as globally (Fig. B6). The effect of N deposition may be due to several mechanisms. Most directly, the addition of N will result in an increase in productivity if N is the limiting nutrient. Nitrogen availability and uptake is critical to photosynthesis and consequently plant growth (Chapin et al. 2011). Nitrogen can also increase allocation of resources to aboveground growth by plants resulting in more aboveground biomass (Levin et al. 1989, Johnson et al. 2008). Over time, species composition can also be altered as a consequence of N addition and the resulting impact on ANPP (Isbell et al. 2013). This result has important implications for how scientists view Earth system functioning. Experimental work has demonstrated the close relationship between N deposition and ANPP, biodiversity, and soil chemistry (Stevens et al. 2004, Clark and Tilman 2008, Bobbink et al. 2010), and earth systems models are beginning to incorporate these dynamics (Zaehle 2013). Because increases in N deposition and atmospheric CO_2 are occurring in parallel over time and can interact in their effect on soil N availability and aboveground productivity, it is particularly important to understand how and where N limits plant response to climate change. While this is an active area of model development, N deposition is not currently included in the majority of Earth system models used by the IPCC (Ciais et al. 2013). Especially given the high global cover of grassland biomes, the influence of N deposition on grassland ANPP demonstrated here should continue to be a focus of development for models of Earth systems in the Anthropocene.

Soil pH was a second important driver of productivity. Soil pH has important influences over the species pool at a given site (Schuster and Diekmann 2003), the availability of nutrients and potentially toxic metals (Tyler and Olsson 2001), and soil the microbial community (Fierer and Jackson 2006). All of these factors could influence the productivity of grassland vegetation. Acid sites were more productive in this model, which is contrary to expectations but may be due to the low frequency of highly acidic sites where we may expect to see lower productivity (mean soil pH 4.02–8.34, only two sites pH < 5.00).

By the year 2050, Dentener (2006) predicts increased N deposition in many parts of the world including South America, southern Africa, and much of Asia. Within these regions are several grasslands of high biodiversity and conservation importance such as the Cerrado and Pampas of South America, the steppe grasslands of Asia, and savannah grasslands of Africa and Asia. In the absence of other limiting factors, we may expect production in these regions to increase in response to additional N deposition with implications for vegetation species composition, land management, and food webs. In areas where deposition is already high, we would expect that further increases in ANPP would be constrained by increased limitation of other resources with the potential for a change to limitation by phosphorus or other factors (Elser et al. 2009). In vegetation dominated by woody species (e.g., forest or woodland ecosystems), experimental evidence for increasing ANPP in response to N deposition is controversial (Magnani et al. 2007, Sutton et al. 2008) but inventory data from across the United States indicates small increases in ANPP during the 1980s and 1990s compared to preindustrial conditions (Thomas et al. 2010). This suggests that increases in ANPP observed here may be more generally applicable.

Depending on the in the impacts of N deposition on the processes associated with carbon cycling, an increase in ANPP with increasing N inputs could contribute to carbon sequestration on a global scale (Pregitzer et al. 2008). Grasslands cover 40% of the Earth's land surface and store approximately 34% of terrestrial ecosystem C (Lal 2001), therefore even small changes in biomass production and the accumulation of carbon in grassland soils could have global consequences. However, evidence to support an increase in carbon storage associated with N deposition in herbaceous systems is currently mixed (Liu and Greaver 2010), partly because the N and C cycles are highly coupled, with N deposition potentially having impacts on both decomposition and productivity, and because these effects are affected by climate (Hyvönen et al. 2007).

The results presented here clearly demonstrate that anthropogenic activities leading to increased N deposition are having a far-reaching effect on our planet. These effects are not captured in standard climatic measures such as MAT or PET, thus, the variation in primary production due to N deposition rates should be explicitly included in future global change models, and examined for its potential consequences for biodiversity, species composition, and other important ecosystem functions.

ACKNOWLEDGMENTS

This work was generated using data from the Nutrient Network experiment, funded at the site scale by individual researchers. Coordination and data management have been supported by funding to E. T. Borer and E. W. Seabloom from the National Science Foundation Research Coordination Network (NSF-DEB-1042132) and Long Term Ecological Research (NSF-DEB-1234162 to Cedar Creek LTER) programs, and the Institute on the Environment (DG-0001-13). We also thank the Minnesota Supercomputer Institute for hosting project data and the Institute on the Environment for hosting Network meetings. C. J. Stevens and E. M. Lind contributed equally to this work.

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Supplemental Material

Ecological Archives

Appendices A and B and a Supplement are available online: http://dx.doi.org/10.1890/14-1902.1.sm