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NITROGEN LIMITATION OF NET PRIMARY PRODUCTIVITY IN TERRESTRIAL ECOSYSTEMS IS GLOBALLY DISTRIBUTED

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Abstract. Our meta-analysis of 126 nitrogen addition experiments evaluated nitrogen (N) limitation of net primary production (NPP) in terrestrial ecosystems. We tested the hypothesis that N limitation is widespread among biomes and influenced by geography and climate. We used the response ratio ($R \cong ANPP_N/ANPP_{ctrl}$) of aboveground plant growth in fertilized to control plots and found that most ecosystems are nitrogen limited with an average 29% growth response to nitrogen (i.e., $R = 1.29$). The response ratio was significant within temperate forests ($R = 1.19$), tropical forests ($R = 1.60$), temperate grasslands ($R = 1.53$), tropical grasslands ($R = 1.26$), wetlands ($R = 1.16$), and tundra ($R = 1.35$), but not deserts. Eight tropical forest studies had been conducted on very young volcanic soils in Hawaii, and this subgroup was strongly N limited ($R = 2.13$), which resulted in a negative correlation between forest R and latitude. The degree of N limitation in the remainder of the tropical forest studies ($R = 1.20$) was comparable to that of temperate forests, and when the young Hawaiian subgroup was excluded, forest R did not vary with latitude. Grassland response increased with latitude, but was independent of temperature and precipitation. These results suggest that the global N and C cycles interact strongly and that geography can mediate ecosystem response to N within certain biome types.

Key words: carbon; meta-analysis; net primary production; nitrogen; nitrogen deposition; nitrogen fertilization; resource limitation.

INTRODUCTION

Nitrogen (N) constrains net primary production (NPP) in terrestrial ecosystems (Vitousek and Howarth 1991). Nitrogen limitation is diagnosed when addition of N results in increased NPP. In this manner, a broad array of ecosystem-scale studies has consistently demonstrated N limitation (Kenk and Fischer 1988, Tamm 1991, Hooper and Johnson 1999). The persistence of N limitation results from the transient nature of biologically available forms of N (Vitousek et al. 2002). Unlike the abiotic inputs of many other resources, the primary source of N is biological N fixation. Once fixed, N is particularly susceptible to being removed from an ecosystem by leaching and volatilization.

Anthropogenic N fertilization of N-limited ecosystems is a primary component of global change. During the 20th century, anthropogenic N fixation doubled the global flux of N to the biosphere. Moreover, N deposition rates are expected to increase another two- or threefold before reaching a plateau (Vitousek et al. 1997, Galloway and Cowling 2002, Lamarque et al. 2005). In contrast to the current pattern of N deposition, which is concentrated in temperate regions of the northeastern United States and northern Europe, future

N deposition will increasingly occur in the tropical regions (Galloway and Cowling 2002, Lamarque et al. 2005). This change in distribution of N deposition will result in N fertilization of a larger proportion and diversity of the earth's ecosystems. However, the effect of this fertilization on global NPP will depend on the degree to which N limits NPP in both temperate and tropical ecosystems.

Walker and Syers (1976) presented a geophysical framework that predicts P limitation should be stronger than N limitation in equatorial regions, owing to considerations of soil age and climate. Warmer and wetter tropical climates enhance N mineralization and plant N use efficiency (Lloyd and Taylor 1994, Schlesinger and Andrews 2000). Concurrently, tropical soils become depleted in P with age (Walker and Syers 1976). By contrast, cold and dry climates reduce N mineralization and plant N use efficiency by slowing enzyme activity (Lloyd and Taylor 1994, Schlesinger and Andrews 2000), while glaciations deliver rocks rich in P and other mineral nutrients to the soil profile. The shift from N to P limitation with soil age has been supported by N and P fertilization studies along a chronosequence in the Hawaiian archipelago (Crews et al. 1995, Vitousek and Farrington 1997). In addition, these global trends are supported by an analysis of plant stoichiometry; both N:C and N:P ratios increase among plants closer to the equator (Reich and Oleksyn 2004). If tropical ecosystems are P limited and N replete, future

FIG. 1.   Global distribution of studies included in the meta-analysis, by biome.

increases in tropical N deposition might not have an important impact on global NPP. Although previous syntheses and reviews support global patterns of nutrient limitation in line with the geophysical hypotheses, no studies have directly tested global patterns of N limitation based on observed plant response to experimental N addition.

To assess global patterns of N limitation, we conducted a meta-analysis of N limitation across diverse biomes. Following the geophysical model (Walker and Syers 1976), we predicted that N limitation would increase poleward and with temperature or precipitation limitation of N mineralization (Vitousek and Howarth 1991, Reich and Oleksyn 2004). To test these predictions, we performed a comprehensive meta-analysis on N addition studies, using the response ratio R as an estimate of the ratio of production in fertilized to control plots.

METHODS

Data selection

We found 80 publications containing 126 independent N addition studies that measured the response of plant productivity to N (Fig. 1 and Appendix A). We included experiments performed on restored prairies and plantations, but excluded greenhouse studies and experiments in which species composition was directly manipulated. Studies were included in our analysis if aboveground NPP (ANPP) was measured on plants that represented 90% or more of the biomass in an ecosystem. Because we

sought to test N limitation directly, we excluded studies that used N deposition or soil fertility gradients as well as studies that lacked an N-only treatment. To meet the statistical assumption of independence among studies, we used only a single measurement from each study; we chose the highest rate of N addition and the first measurement of productivity one or more years after fertilization. Choosing the maximum fertilization rate increased the likelihood that N was available in excess of plant demand. Using the initial time step reduced downstream feedbacks of excess N associated with either N saturation (Aber et al. 1998) or species replacement (Chapin et al. 1986). We assumed studies conducted at distinct sites were independent; we also assumed independence of discrete studies performed in the same general area or research station.

Most data were obtained from the original article. When data were presented in graphical format, we used the Grab It! graph digitizer (Datatrend Software, Raleigh, North Carolina, USA) to derive numerical data. We assumed that unidentified error bars were standard errors. Data were occasionally presented as subgroups within a plot, for example, by species or functional group. To combine subgroup data into a single value for the plant community response, means were added together and the standard deviation was calculated as the square root of the sum of standard deviations (conservatively assuming independence of subgroups [Gurevitch et al. 2000]).

We assigned each study to one of seven biomes (Table 1), with grasslands and forests divided into tropical or

temperate, depending on latitude. As necessary, we obtained study data from secondary sources including the author, other reports at the same location, and public databases. For example, NASA WorldWind provided geographical coordinates based on a site name or description (information *available online*).[4] Based on the geographical coordinates, we found mean annual temperature (MAT) and mean annual precipitation (MAP) from local weather stations or at the nearest point in the New et al. (2002) global $0'10'' \times 0'10''$ climatology (see Supplement).

Plant productivity and the response ratio

The response ratio (R) is the ratio of estimated ANPP in the fertilized and control plots: $R = \text{ANPP}_N/\text{ANPP}_{ctrl}$. We calculated the natural log of R, $\ln(R)$, from each study to obtain a single unitless response metric, and this metric enabled us to combine estimates of ANPP from multiple methods into a single meta-analysis (Hedges et al. 1999). Methods used to estimate NPP were diverse. Forest productivity fit into five categories: allometric biomass increment plus litterfall (ANPP*), basal area increment (BAI), diameter increment (DI), annual litterfall, and allometric volume increment. Peak aboveground biomass or repeated measurements were used to estimate current-year production in the herbaceous plant communities of grasslands and wetlands. Most of these measurements accounted for biomass increments but not carbon lost to herbivory, decomposition, turnover, volatile organic compounds, root exudates, and allocation to microbial symbionts. Previous reviews discuss the methods and assumptions associated with NPP measurements in more detail (Clark 2002, Scurlock et al. 2002, Chapin et al. 2005). Although belowground NPP (BNPP) accounts for approximately half of total NPP (Schimel 1995, Saugier et al. 2001, Giardina et al. 2005), BNPP is infrequently measured. Consequently, the present analysis is limited to ANPP by the available data. Although N may increase the ratio of above- to belowground biomass (Chapin 1980, Bloom et al. 1985, Agren and Franklin 2003), we have no reason to suspect that an observed increase in ANPP could be offset by a decrease in BNPP. In fact, N increased BNPP ($R = 1.47, n = 7, P = 0.03$) among the four forests and three grasslands in which it was measured (Owensby et al. 1994, Ostertag 2001, Camill et al. 2004, Davis et al. 2004).

Statistics

First, we combined results from independent studies in a meta-analysis to test the overall response using a weighted, random-effects model. Next, categorical effects, including biome, fertilizer form, and method of measurement, were compared using a weighted, mixed-effects model (Hedges et al. 1999, Rosenberg et al. 2000, 2004). These models incorporate both within- and among-study variance into study weights to account

for real differences that exist among independent studies. Calculation of R required treatment and control means, and study weights used in the analysis required within-study replication and an estimate of the standard deviation (s). We derived s from multiple variance estimates. Standard error (s_x) was most often reported, and s could be calculated as $s = s_x\sqrt{n}$. When the effect of nitrogen was not significant and s_x was not reported, s was calculated across treatments. Otherwise, it was possible to estimate s from ANOVA tables. For example, an estimate for s may be derived from the mean squared error ($s \cong \sqrt{\text{MSE}}$) or least significant difference ($s \cong \text{LSD}^2/t_{\alpha/2}^2$) ($t_{\alpha/2}^2$ is calculated from a two-tailed t distribution at significance level α; Rosenberg et al. 2004). We can also estimate s when given the significance level, P, along with treatment and control means (X_T and X_C) and treatment and control degrees of freedom ($s \cong (X_T - X_C)/t_{(P/2,df)}$). Compared to a directly calculated treatment variance, these estimates resulted in an overestimation of variance, providing less weight for those studies in the analysis. All statistical analyses were computed with Comprehensive Meta-Analysis software (Borenstein and Rothstein 1999).

Preferential publication of significant results can be a source of bias in meta-analysis (Gurevitch and Hedges 1999). However, this bias is minimized when the result of interest is part of a larger investigation. This would limit the bias in the present analysis, because three-quarters (97) of the studies reported data from phosphorus addition, multiple rates of N addition, and/or multiple years after fertilization. We used two statistical metrics to infer publication bias. The trim-and-fill method uses the correlation between standard error and effect size to impute studies omitted due to bias (Duval and Tweedie 2000), and the fail-safe N calculates the number of zero-effect studies that would be required to invalidate our findings (Rosenthal 1979).

Both overall and categorical results are reported as R, along with 95% confidence intervals, degrees of freedom, model variance (Q), and the significance level (P). Therefore, fertilization effects were significant at $P = 0.05$ if confidence intervals do not include $R = 1$. Effects of MAT, MAP, and latitude on R were tested using a weighted, unrestricted maximum-likelihood meta-regression model (Borenstein and Rothstein 1999). We performed climate and geographical regressions. In order to derive global-scale patterns in these regressions, we combined temperate and tropical subclasses. For significant correlations, we report significance (P), slope (m), intercept (b), variance accounted for by the model (Q_w), and total variance (Q_{tot}).

RESULTS

Five of seven biomes were represented by 10 or more studies (Table 1, Fig. 1). Nitrogen addition increased plant growth across all biomes by 29% ($P < 0.0001$; Table 1), and all biomes except for desert responded positively to N fertilizer addition. Furthermore, the

TABLE 1. Effects of nitrogen on plant growth, overall and grouped by biome.

Grouping	n	R	95% CI	Q	P
Overall	126	1.29	1.22–1.35	1032	<0.0001
Biome	7			20.5	0.0022
Temperate forest	22	1.19	1.11–1.28		<0.0001
Tropical forest	16	1.60	1.30–1.97		<0.0001
Excluding young Hawaiian soils	8	1.20	1.04–1.40		0.013
Young Hawaiian soils	8	2.13	1.48–3.08		<0.0001
Tundra	10	1.35	1.12–1.64		0.0018
Tropical grassland	6	1.26	1.04–1.54		0.021
Desert	3	1.11	0.80–1.55		0.53
Temperate grassland	32	1.53	1.37–1.71		<0.0001
Wetland	36	1.16	1.00–1.34		0.045

Notes: The response ratio, R, is the ratio of estimated aboveground net primary productivity in the fertilized to the control plots. An $R > 1$ reflects a positive growth response to nitrogen and indicates nitrogen limitation as defined in *Methods*. The homogeneity statistic Q is used to assess homogeneity of effect sizes. Boldface type indicates responses that are significant at $P < 0.05$.

magnitude of the response varied by biome ($P = 0.0018$). Temperate grassland response ($R = 1.53$) and tropical grassland response ($R = 1.26$) were not significantly different ($P = 0.10$) from one another. Tropical forest response ($R = 1.60$) was greater than temperate forest response ($R = 1.19$, $P = 0.011$). Eight of the 16 tropical forest studies were performed on very young (<1000 yr) Hawaiian soils specifically chosen as ecosystems that should be prone to N limitation (P. M. Vitousek, *personal communication*). Aboveground net primary production on the young Hawaiian soils doubled after N addition ($R = 2.13$, $P < 0.0001$). After removing these studies, the response of tropical forests ($R = 1.20$; N effect, $P = 0.013$) was similar to that of temperate forests (tropical vs. temperate, $P = 1.00$).

Dependence of R on geography and climate

Across all studies, correlation with latitude was not significant ($P = 0.10$, Table 2). Nevertheless, response varied among biomes. Forest R decreased poleward, whereas grassland and wetland R increased (Fig. 2a–c). The response ratio increased with MAP and MAT across forest studies ($P = 0.033$; Fig. 2d, f) and with MAT across tundra studies ($P = 0.015$; Fig. 2g). The response ratio decreased with MAP in wetlands ($P = 0.007$; Fig. 2e). All other correlations were nonsignificant (Table 2).

Experimental variables

Duval and Tweedie's (2000) trim and fill method predicted that no studies were missing due to publication bias, and our fail-safe N (Rosenthal 1979) was over 21 000, indicating 150 zero-effect studies would be required for each study in the present analysis to invalidate our result (expand the 95% confidence interval to include $R = 1$).

Nitrogen was applied in five different chemical forms and combinations thereof (Appendix B). Ammonium nitrate (NH_4NO_3) was added in over half the studies ($n = 72$), and urea was applied in one-fifth ($n = 24$). Neither the type of fertilizer ($n = 8$, $P = 0.30$) nor the oxidation status of the N (oxidized, reduced, or combined, $P = 0.46$) had significant effects on R. Regressions on N application rate and on the duration of fertilization (i.e., time between fertilization and time of measurement) were nonsignificant ($P = 0.42$ and $P = 0.79$, data not shown). However, these tests were biased by our selection of the highest rate of application and shortest time interval from each study.

Within forests, litterfall alone did not significantly respond to N addition (Appendix B). The response ratios that were calculated based on tree trunk increments of diameter, basal area, or volume were generally higher on average than those based on litterfall alone, but were not different from estimates based on combined trunk increment and litterfall response. Basal area increment was reported more often in temperate forests, while diameter increment was reported more often in tropical forests, accounting for the larger response of DI-based estimates. Grassland and wetland measurements were categorized as either repeated measurements or peak-season biomass. Results based on these two methods did not significantly differ ($P = 0.18$).

DISCUSSION

Global N limitation

Nitrogen limits ANPP in the majority of terrestrial ecosystems. Our results demonstrate consistent and statistically significant responses of ecosystem NPP to N addition (Table 1), supporting the hypothesis that N limitation is widespread (Vitousek and Howarth 1991). We focus on N limitation because increasing N availability is a major component of global change (Vitousek and Howarth 1991). However, other nutrients stimulate NPP, and responses to N in combination with other nutrients exceed responses to N alone (Harpole et al. 2007; Elser et al. 2007). Therefore, our estimates of R should be considered conservative with respect to nutrient limitation overall.

TABLE 2. Correlations between R and environmental variables expressed as the change in response R per unit latitude, temperature, or precipitation (statistics used for Fig. 2).

Regressions	n	Slope	Q_w	Q_{tot}	P
Latitude ΔR/degrees latitude					
Overall	124		2.8	141.5	0.10
Wetlands	35	0.076	16.7	55.0	<**0.0001**
Forests	38	−0.0046	4.5	65.3	**0.033**
Excluding young Hawaiian soils	30		0.0	30.2	0.93
Grasslands	35	0.0080	5.9	53.8	**0.015**
Tundra	9		2.6	19.7	0.11
MAT ΔR/°C					
Overall	124		3.5	141.3	0.060
Wetlands	35		0.9	46.6	0.34
Forests	38	0.14	6	67.1	**0.014**
Excluding young Hawaiian soils	30		1.5	29.7	0.22
Grasslands	35		0.5	46.9	0.46
Tundra	9	0.038	5.7	20.9	**0.017**
MAP ΔR/(mm/yr)					
Overall	124		2.3	141.3	0.13
Wetlands	35	−0.00085	7.4	46.4	**0.0070**
Forests	38	0.012	9.3	55.9	**0.0018**
Excluding young Hawaiian soils	30		0.02	30.4	0.88
Grasslands	35		0	48.0	1.00
Tundra	9		2.4	19.6	0.12

Notes: The response ratio, R, is the ratio of estimated aboveground net primary productivity in the fertilized to the control plots (an $R > 1$ reflects a positive growth response to nitrogen and indicates nitrogen limitation as defined in *Methods*); Q_w is the variance accounted for by the regression model; Q_{tot} is the total variance among studies included in the regression; MAT is mean annual temperature; MAP is mean annual precipitation. Boldface type indicates regressions that are significant at $P < 0.05$.

Forests

In contrast to the prediction by Walker and Syers (1976) and indirect evidence (Reich and Oleksyn 2004) that the degree of N limitation increases with latitude, we observed no trend in forest R when eight very young sites from Hawaii were removed (Table 2) and a poleward decrease when they were included (Fig. 2a). We therefore conclude that N limitation is an important control on NPP even in tropical forests. However, these findings may not reflect tropical forests as a whole. Among the eight studies that were not established on young Hawaiian lava flows, four were conducted in lowland (<1000 m) tropical forests. Of these four, one was a primary forest (Mirmanto et al. 1999) that was N replete ($R = 1.09$, $P = 0.64$). The remaining three were based in secondary lowland tropical forests (Campo and Vázquez-Yanes 2004, Davidson et al. 2004) that were N limited ($R = 1.50$, $P = 0.007$). Secondary forests represent 40% of tropical forests (Brown and Lugo 1990, FAO 1995), so N limitation in these ecosystems would have substantial impacts on global NPP.

Grasslands

Although grassland R increased with latitude, there was no correlation between R and MAT or MAP (Table 2). These results support the conclusion that grassland R is independent of climate over wide ranges (Schimel et al. 1997, Hooper and Johnson 1999). Hooper and Johnson (1999) analyzed the results of 40 arid to semi-arid (MAP = 211–1031 mm/yr) grassland N-addition

studies, including multiple time points and fertilization rates from each study, and observed no correlation between R and geographical or temporal variation in precipitation. Eight of our 38 grassland data points were included in the previous study.

The CENTURY model (Schimel et al. 1997) predicts tight coupling of water and N limitation. This occurs because both soil N availability and plant N demand are limited by, and therefore positively correlated to, temperature and water availability. According to CENTURY (Schimel et al. 1997), this causes the ratio of N availability to plant N demand to remain constant as temperature and precipitation increase. By corollary, the ratio of N deficit (demand − supply) to N demand would also remain constant. If plant response to N is proportional to the N deficit while plant N demand is proportional to NPP, R should also remain constant as temperature and precipitation increase. Our finding that grassland R remains constant across a large range of MAT and MAP supports the CENTURY prediction (Schimel et al. 1997) and corroborates the results reported by Hooper and Johnson (1999).

Wetlands

Although the mean response of wetland ANPP to N was positive (Table 1), 11 of the 36 wetlands responded negatively to N. Previous research has demonstrated that wetland NPP can be limited by resources other than N, most commonly P (Verhoeven et al. 1996, Bedford et al. 1999, Olde Venterink et al. 2001). For example,
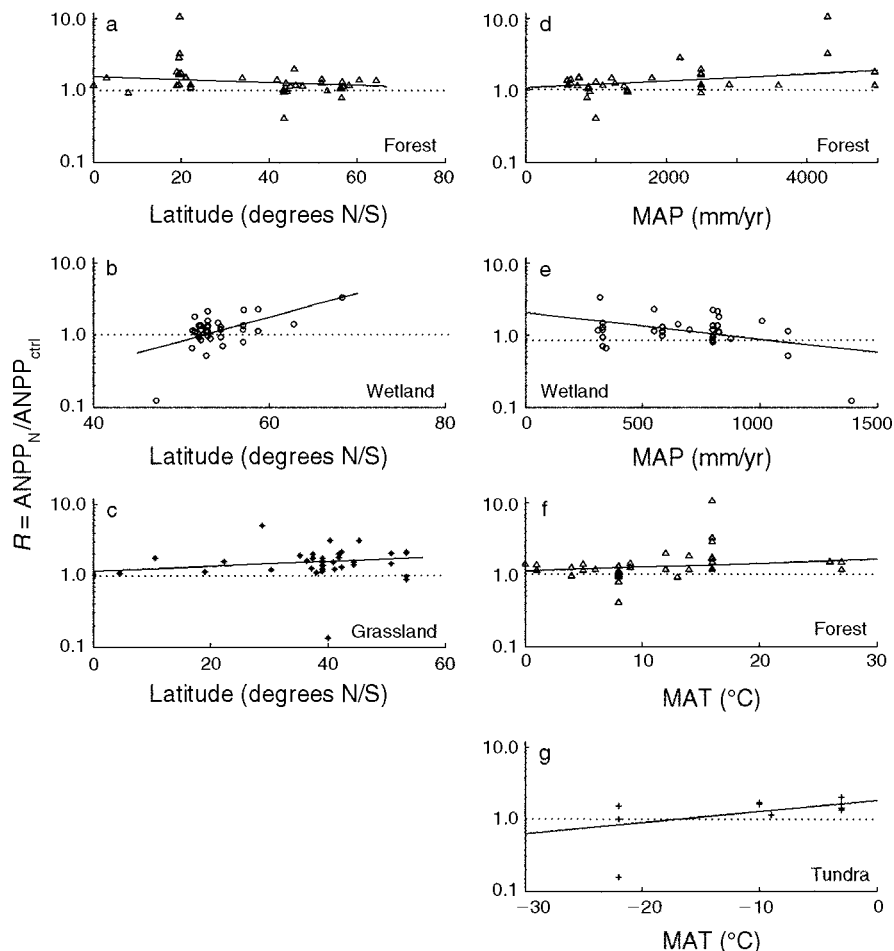
FIG. 2. (a–c) Correlations between the response ratio (R) and absolute latitude among (a) forest, (b) wetland, and (c) grassland studies. The wetland regression remains significant after removal of the maximum or the minimum value of R. (d, e) Correlations between R and mean annual precipitation (MAP) among (d) forest and (e) wetland studies. The tundra regression is not significant after removal of the minimum value of R. (f, g) Correlations between R and mean annual temperature (MAT) among (f) forest and (g) tundra studies. For statistics see Table 2.

wetlands that experience high rates of N deposition, are at a late successional stage, or have cation-rich water inputs are more likely to exhibit P rather than N limitation (Morris 1991, Verhoeven and Schmitz 1991, Aerts et al. 1992). These results illustrate how the biogeochemistry of wetlands can differ from that of well-drained grasslands.

The negative correlation between wetland R and MAP (Table 2, Fig. 2e) is consistent with the conclusion of Morris (1991) that the impact of N deposition on a wetland is correlated to the contribution of rainfall to its water budget. Although precipitation is linked to N deposition, plant N demand may decrease with precipitation. Plant growth is limited by anaerobic conditions, and these conditions persist longer in wetlands with high rainfall (Morris 1991). Furthermore, rain-fed wetlands are more likely to be limited by other nutrients that are delivered via ground or surface water inputs.

Potential impacts on the global carbon cycle

The response of plants to N addition is an indication of the global NPP deficit that can be attributable to N limitation. However, we do not expect that long-term N deposition will produce the same NPP response that was observed in the N fertilization studies. Experimental nitrogen addition provides an ecosystem with an immediate and large increase in N availability. In the present analysis, the rate of N addition was 14.3 ± 1.1 g $N \cdot m^{-2} \cdot yr^{-1}$ (mean $\pm$ SE). In contrast, anthropogenic pollution produces a steadily increasing rate of N deposition from pre-industrial levels. Presently, anthropogenic N inputs average 1 g $N \cdot m^{-2} \cdot yr^{-1}$ over terrestrial ecosystems and could level off at 4–6 g $N \cdot m^{-2} \cdot yr^{-1}$ during the next century (Prather et al. 2001, Galloway and Cowling 2002, Lamarque et al. 2005). On average, we found a 30% increase in NPP under N addition, and at the global scale this is equivalent to an NPP response of 20×10^{15} g C/yr (calculated using R from Table 1 and

global NPP estimates for each biome; Houghton and Skole 1990, Saugier et al. 2001). However, our data set represents short-term data that are not necessarily applicable to persistent low-level N deposition. Global models estimate that the present impact of anthropogenic N fertilization on global NPP is closer to $0.5–1.5 \times 10^{15}$ g C/yr (Townsend et al. 1996, Vitousek et al. 1997). Furthermore, there is evidence that long-term exposure to pollution can negatively impact plant growth as a system becomes N saturated and the soil becomes acidified (Aber et al. 1998).

Ultimately, the balance between production and decomposition determines the impact of N on the net global flux of carbon from the biosphere to the atmosphere. Anthropogenic N can augment terrestrial carbon storage by increasing NPP more than decomposition (Vitousek et al. 1997). Our study supports this proposition by demonstrating strong, consistently positive effects of N on NPP in contrast to the inconsistent effects of N on decomposition (Fog 1988). Nitrogen can increase, decrease, or have no effect on the rate of decomposition, depending on environmental conditions, substrate quality, and microbial physiology (Schlesinger and Andrews 2000). For example, a meta-analysis of litter decomposition experiments by Knorr et al. (2005) found no significant effect of N on litter decomposition overall. In regions exposed to high rates of N deposition, experimental N addition either decreased or had no effect on decomposition rates (Knorr et al. 2005). Conversely, N limits NPP even among ecosystems in our meta-analysis that were exposed to high background rates of N deposition.

Methodological considerations

Studies of N limitation are not randomly distributed (Fig. 1), and our conclusions are necessarily limited to the studies included in our analysis. Although we found no evidence for publication bias (unpublished zero-effect studies), research bias is more difficult to detect. Research bias results from experiments not performed because no effect is expected (Gurevitch and Hedges 1999). For example, many tropical forest studies used NPK fertilizer rather than N fertilizer, because tropical forests are often expected to be P limited. We were unable to include the NPK studies in our meta-analysis.

Additionally, published research is geographically clustered around universities and well-studied ecosystems. This geographical bias is particularly evident in the cluster of tropical forest studies performed in Hawaii and to a lesser degree among grasslands in midwestern United States. Equally notable is the scarcity of available studies performed in low-latitude deserts, grasslands, and forests, particularly in Africa, South America, and Asia (Fig. 1). The least-studied regions will experience disproportionate increases in N deposition in the near future. A better understanding of the interaction among nitrogen, climate, and plant physiology in these ecosystems will provide a more detailed

understanding of how future N deposition will affect the global C balance.

We found no significant effects due to methodological differences among studies (Appendix B), demonstrating the utility of the log response ratio for comparison among studies. The type of fertilizer and rate at which it is applied, estimates of ANPP, and the lag between initial fertilization and initial measurement did not influence R. We conclude that fertilizer form is not an important factor. However, it is not possible to infer that there is no effect of time or fertilization rate because of our data selection bias (see *Methods*).

CONCLUSIONS

Nitrogen limitation constrains productivity in most ecosystems, and the degree of limitation varies by biome (Table 1). Response was correlated with latitude, MAT, or MAP within some biomes but not overall (Table 2). Our findings support the prediction that N limitation is widespread (Vitousek and Howarth 1991), but do not rule out multiple element limitation (Rastetter and Shaver 1992, Harpole et al. 2007; Elser et al. 2007). Evidence for the poleward increase in the degree of N limitation as predicted by the geophysical hypothesis (Walker and Syers 1976) was observed in grasslands and wetlands, but not in forests. Nitrogen limitation is important in many tropical forests, montane as well as secondary lowland forests. Primary lowland tropical forests were represented by a single study, leaving the potential response to N by a large fraction of terrestrial NPP difficult to predict. Historically elevated N deposition may suppress R in temperate regions, possibly overwhelming the geophysical mechanisms outlined by Walker and Syers (1976). Increasing N deposition, particularly in the most rapidly developing regions, is likely to further stimulate global NPP and slow the accumulation of atmospheric CO_2.

LITERATURE CITED

Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate

forest ecosystems—hypotheses revisited. BioScience 48:921–934.

Aerts, R., B. Wallen, and N. Malmer. 1992. Growth-limiting nutrients in sphagnum-dominated bogs subject to low and high atmospheric nitrogen supply. Journal of Ecology 80:131–140.

Agren, G. I., and O. Franklin. 2003. Root : shoot ratios, optimization and nitrogen productivity. Annals of Botany 92:795–800.

Bedford, B. L., M. R. Walbridge, and A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151–2169.

Bloom, A. J., F. S. Chapin, and H. A. Mooney. 1985. Resource limitation in plants—an economic analogy. Annual Review of Ecology and Systematics 16:363–392.

Borenstein, M., and H. Rothstein. 1999. Comprehensive meta-analysis. Biostat, Englewood, New Jersey, USA.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. Journal of Tropical Ecology 6:1–32.

Camill, P., et al. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications 14:1680–1694.

Campo, J., and C. Vázquez-Yanes. 2004. Effects of nutrient limitation on aboveground carbon dynamics during tropical dry forest regeneration in Yucatán, Mexico. Ecosystems 7:311–319.

Chapin, F. S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11:233–260.

Chapin, F., P. Vitousek, and K. van Cleve. 1986. The nature of nutrient limitation in plant communities. American Naturalist 127:48–58.

Chapin, F., G. Woodwell, J. Randerson, G. Lovett, E. Rastetter, D. Baldocchi, D. Clark, M. Harmon, D. Schimel, and R. Valentini. 2005. Reconciling carbon-cycle concepts, terminology, and methodology. Ecosystems 9:1041–1050.

Clark, D. A. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. Ecological Applications 12:3–7.

Crews, T. E., K. Kitayama, J. H. Fownes, R. H. Riley, D. A. Herbert, D. Muellerdombois, and P. M. Vitousek. 1995. Changes in soil-phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76:1407–1424.

Davidson, E. A., C. J. R. de Carvalho, I. C. G. Vieira, R. O. Figueiredo, P. Moutinho, F. Y. Ishida, M. T. P. dos Santos, J. B. Guerrero, K. Kalif, and R. T. Sabá. 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecological Applications 14(Supplement):S150–S163.

Davis, M. R., R. B. Allen, and P. W. Clinton. 2004. The influence of N addition on nutrient content, leaf carbon isotope ratio, and productivity in a Nothofagus forest during stand development. Canadian Journal of Forest Research 34:2037–2048.

Duval, S., and R. Tweedie. 2000. Trim and fill: a simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. Biometrics 56:455–463.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine, and terrestrial ecosystems. Ecology Letters 10:1135–1142.

FAO [Food and Agricultural Organization of the United Nations]. 1995. Forest resources assessment 1990: global synthesis. FAO Forestry Paper Number 124. FAO, Rome, Italy.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic-matter. Biological Reviews of the Cambridge Philosophical Society 63:433–462.

Galloway, J., and E. Cowling. 2002. Reactive nitrogen and the world: 200 years of change. Ambio 31:64–71.

Giardina, C., M. Coleman, D. Binkley, J. Hancock, J. King, E. Lilleskov, W. Loya, K. Pregitzer, M. Ryan, and C. Trettin. 2005. The response of belowground carbon allocation in forests to global change. Pages 120–154 in D. Binkley and O. Menyailo, editors. The impacts of global climate change on plant–soil interactions. NATO Science Series. Kluwer Academic Press, Dordrecht, Germany.

Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology 80:1142–1149.

Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. American Naturalist 155:435–453.

Harpole, W. S., L. Goldstein, and R. Aicher. 2007. Resource limitation. Pages 119–127 in M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. California grasslands: ecology and management. University of California Press, Berkeley, California, USA.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Hooper, D. U., and L. Johnson. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. Biogeochemistry 46:247–293.

Houghton, R. A., and D. L. Skole. 1990. Carbon. Pages 393–408 in B. L. Turner, W. C. Clark, J. F. Kates, J. T. Matthews, and W. B. Meyer, editors. The earth as transformed by human action. Cambridge University Press, Cambridge, UK.

Kenk, G., and H. Fischer. 1988. Evidence from nitrogen-fertilization in the forests of Germany. Environmental Pollution 54:199–218.

Knorr, M., S. Frey, and P. Curtis. 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86:3252–3257.

Lamarque, J., J. Kiehl, G. P. Brasseur, T. Butler, P. Cameron-Smith, W. Collins, W. Collins, C. Granier, D. Hauglustaine, and P. Hess. 2005. Assessing future nitrogen deposition and carbon cycle feedback using a multimodel approach: analysis of nitrogen deposition. Journal of Geophysical Research 110:D19303 [Online: doi:10.1029/2005JD005825].

Lloyd, J., and J. Taylor. 1994. On the temperature dependence of soil respiration. Functional Ecology 8:315–323.

Mirmanto, E., J. Proctor, J. Green, and L. Nagy. 1999. Effects of nitrogen and phosphorus fertilization in a lowland evergreen rainforest. Philosophical Transactions of the Royal Society B 354:1825–1829.

Morris, J. 1991. Effects of nitrogen loading on wetland ecosystems with particular reference to atmospheric deposition. Annual Review of Ecology and Systematics 22:257–279.

New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. Climate Research 21:1–25.

Olde Venterink, H., R. E. van der Vliet, and M. J. Wassen. 2001. Nutrient limitation along a productivity gradient in wet meadows. Plant and Soil 234:171–179.

Ostertag, R. 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. Ecology 82:485–499.

Owensby, C., L. Auen, and P. Coyne. 1994. Biomass production in a nitrogen-fertilized, tallgrass prairie ecosystem exposed to ambient and elevated levels of CO_2. Plant and Soil 165:105–113.

Prather, M., D. Ehhalt, F. Dentener, R. G. Derwent, E. Dlugokencky, E. Holland, I. S. A. Isaksen, J. Katima, V. Kirchhoff, P. Matson, P. M. Midgley, and M. Wang. 2001. Atmospheric chemistry and greenhouse gases. Pages 239–287 in J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson,

editors. Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, UK.

Rastetter, E. B., and G. R. Shaver. 1992. A model of multiple-element limitation for acclimating vegetation. Ecology 73: 1157–1174.

Reich, P., and J. Oleksyn. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proceedings of the National Academy of Sciences 101:11001–11006.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin: statistical software for meta-analysis. Version 2. Sinauer Associates, Sunderland, Massachusetts, USA.

Rosenberg, M. S., K. A. Garrett, Z. Su, and R. L. Bowden. 2004. Meta-analysis in plant pathology: synthesizing research results. Phytopathology 94:1013–1017.

Rosenthal, R. 1979. The "file drawer problem" and tolerance for null results. Psychological Bulletin 86:638–641.

Saugier, B., J. Roy, and H. Mooney. 2001. Estimations of global terrestrial productivity: Converging toward a single number? Pages 543–557 in J. Roy, B. Saugier, and H. A. Mooney, editors. Terrestrial global productivity: past, present, and future. Academic Press, San Diego, California, USA.

Schimel, D. S. 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1:77–91.

Schimel, D. S., B. H. Braswell, and W. J. Parton. 1997. Equilibration of the terrestrial water, nitrogen, and carbon cycles. Proceedings of the National Academy of Sciences (USA) 94:8280–8283.

Schlesinger, W. H., and J. A. Andrews. 2000. Soil respiration and the global carbon cycle. Biogeochemistry 48:7–20.

Scurlock, J. M. O., K. Johnson, and R. J. Olson. 2002. Estimating net primary productivity from grassland biomass dynamics measurements. Global Change Biology 8:736–753.

Tamm, C. 1991. Nitrogen in terrestrial ecosystems: questions of productivity, vegetational changes, and ecosystem stability. Springer-Verlag, Heidelberg, Germany.

Townsend, A. R., B. H. Braswell, E. A. Holland, and J. E. Penner. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. Ecological Applications 6:806–814.

Verhoeven, J. T. A., W. Koerselman, and A. F. M. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology and Evolution 11: 494–497.

Verhoeven, J. T. A., and M. B. Schmitz. 1991. Control of plant growth by nitrogen and phosphorus in mesotrophic fens. Biogeochemistry 12:135–148.

Vitousek, P., J. Aber, R. Howarth, G. Likens, P. Matson, D. Schindler, W. Schlesinger, and D. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7:737–750.

Vitousek, P. M., and H. Farrington. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37:63–75.

Vitousek, P. M., S. Hattenschwiler, L. Olander, and S. Allison. 2002. Nitrogen and nature. Ambio 31:97–101.

Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea—How can it occur? Biogeochemistry 13:87–115.

Walker, T. W., and J. K. Syers. 1976. Fate of phosphorus during pedogenesis. Geoderma 15:1–19.

APPENDIX A

Study statistics and site variables used in the meta-analysis, including biome classification, climate, latitude, and statistics calculated for the analysis, with references (*Ecological Archives* E089-020-A1).

APPENDIX B

Effect of nitrogen form and method of aboveground net primary productivity estimation on *R* (*Ecological Archives* E089-020-A2).

SUPPLEMENT

MATLAB m-code used to obtain values of mean annual temperature and mean annual precipitation at a point nearest to the study site from the New et al. (2000) 10′ climatology when local data were not available (*Ecological Archives* E089-020-S1).