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Review

Nitrogen limitation in arid-subhumid ecosystems: A meta-analysis of fertilization studies

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ABSTRACT

Evidence supporting water limitation in arid-semiarid ecosystems includes strong correlations between aboveground net primary production (ANPP) and annual precipitation as well as results from experimental water additions. Similarly, there is evidence of N limitation on ANPP in low precipitation ecosystems, but is this a widespread phenomenon? Are all arid-semiarid ecosystems equally limited by nitrogen? Is the response of N fertilization modulated by water availability?

We conducted a meta-analysis of ANPP responses to N fertilization across arid to subhumid ecosystems to quantify N limitation, using the effect-size index *R* which is the ratio of ANPP in fertilized to control plots. Nitrogen addition increased ANPP across all studies by an average of 50%, and nitrogen effects increased significantly ($P = 0.03$) along the 50–650 mm yr^{-1} precipitation gradient. The response ratio decreased with mean annual temperature in arid and semiarid ecosystems but was insensitive in subhumid systems. Sown pastures showed significant ($P = 0.007$) higher responses than natural ecosystems. Neither plant-life form nor chemical form of the applied fertilizer showed significant effects on the primary production response to N addition. Our results showed that nitrogen limitation is a widespread phenomenon in low-precipitation ecosystems and that its importance increases with annual precipitation from arid to subhumid regions. Both water and N availability limit primary production, probably at different times during the year; with frequency of N limitation increasing and frequency of water limitation decreasing as annual precipitation increases. Expected increase N deposition, which could be significant even in arid ecosystems, would increase aboveground net primary production in water-limited ecosystems that account for 40% of the terrestrial surface.

1. Introduction

Is water availability the sole limiting factor of primary productivity in arid-subhumid ecosystems? Or is nitrogen availability another frequent limiting factor? Ecologists have argued about answers to these questions for some time (Burke et al., 1997; Hooper and Johnson, 1999, West and Skujins, 1978). Primary production in low-precipitation ecosystems is controlled mainly by precipitation inputs, which is evidenced by strong correlations ($r^2 \geq 90$) between aboveground net primary production (ANPP) and annual precipitation in space at regional and global scales (for example Rosenzweig, 1968; Sala et al., 1988). Similarly, manipulative experiments provided support for a causal relationship between water availability and ANPP (Chou et al., 2008; Robertson et al., 2009; Yahdjian and Sala, 2006). The relationship between ANPP and precipitation through time seems to be weaker with annual precipitation accounting for only 25–30% of interannual variability in ANPP (Lauenroth and Sala, 1992). There is also evidence of N limitation of ANPP in low precipitation ecosystems (Ettershank et al., 1978; Fisher et al., 1988; Hooper and Johnson, 1999, West and Skujins, 1978).

Nitrogen limitation becomes evident when nitrogen fertilization results in increases in ANPP. Experiments assessing the effect of nitrogen fertilization on productivity in water-limited ecosystems showed contradictory results (Ettershank et al., 1978; Fisher et al., 1987). The great variety of fertilization methods like nitrogen addition rates and timing, chemical forms, moisture conditions, vegetation life forms and the use of appropriate statistical tools may contribute to these different results. The first attempt to synthesize fertilization results in arid regions used

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a biased sample of studies, ad-hoc indices and traditional statistical approaches that yielded inconclusive results (Hooper and Johnson, 1999). The limited information from locations in the upper end of the precipitation gradient skewed the results as many of the analysis reported by Hooper and Johnson (1999) were strongly influenced by the response of only one site with 800 mm of mean annual precipitation. Modern meta-analysis techniques offer formal statistical methods for comparing and integrating results of multiple studies (Arnqvist and Wooster, 1995; Osenberg et al., 1999) and have been recently implemented in ecological studies (Knorr et al., 2005; LeBauer and Treseder, 2008; Liao et al., 2008). For instance, LeBauer and Treseder (2008) evaluated nitrogen limitation of net primary production in terrestrial ecosystems at the global scale and found that N limitation was globally distributed. However, they could not find a positive response of primary production to N addition in desert biomes for which they had only 3 studies. Also, Elser et al. (2007) evaluated nitrogen and phosphorus limitation in terrestrial, freshwater, and marine ecosystems but they did not include arid nor desert ecosystems where interactions with water availability may be important.

We hypothesize that nitrogen limitation is indeed widespread across arid and semiarid ecosystems. In order to test this hypothesis, we need to answer the following questions. Does nitrogen limit ANPP in arid to subhumid ecosystems and how large is the overall N limitation? Do ANPP responses to N addition change along the annual precipitation gradient from arid to subhumid? Do ANPP responses to N addition change along temperature gradients? Are vegetation responses in sown pastures higher than responses in natural ecosystems? And within natural ecosystems, do responses differ as a function of dominant plant life forms? Do N forms of fertilizer (i.e. urea vs. ammonium nitrate) and doses affect ANPP responses?

Our objective was to answer these questions using meta-analysis of ANPP responses to N fertilization across arid to subhumid ecosystems worldwide. We performed the analysis calculating the response ratio *R* (Hedges et al., 1999) as an estimate of the ratio of aboveground net primary production in fertilized to control plots.

2. Materials and methods

2.1. Data sources

We included in this study 52 publications containing 68 independent N fertilization experiments that measured the response of ANPP to N fertilization (Supporting Information). We searched studies in the Web of knowledge$^{(SM)}$ using nitrogen fertilization, nitrogen manipulations, and nitrogen limitations as keywords. We included 17 studies used by Hooper and Johnson (1999), 3 by Elser et al. (2007), and 10 by LeBauer and Treseder (2008). To be included in the meta-analysis, the site where the experiment was carried out had to have a mean annual precipitation/potential evapotranspiration (MAP/PET) ratio ranging from 0.05 to 0.75, which corresponds to arid-subhumid categories as defined by Le Houérou (1996). The range in MAP was between 50 and 650 mm per year, and mean annual temperature (MAT) between 2 and 26 °C. Nitrogen fertilization studies also had to report some measure of ANPP in control and fertilized treatments, along with measures of deviation (standard error, standard deviation or confidence interval), and sample size. Most studies estimated ANPP as peak biomass, which is the most common way of estimating ANPP (Sala and Austin, 2000). We excluded studies in crops, as well as studies that applied at the same time other resources, i.e. phosphorus or water as a mixture treatment. We included experiments in pastures where grasses were sown. When several fertilizer doses were used in the same study, we selected the highest rate of N addition, and when several years were informed, we used the average response during years. We restricted the analysis to studies in which N addition occurred in the years of production measurements. Most data were obtained from the original article, sometimes extracted from graphical format. Climate variables such as mean annual precipitation, mean annual temperature, and latitude were obtained from the original article when informed. If not, climate variables were extracted from the Worldclim database version 1.4 with ArcGIS Desktop 9.2, and MAP/PET ratios were calculated with the same software. Soil characteristics (texture, pH, organic carbon, e.g.) were extracted from the Harmonized World Soil Database (version 1.1) (FAO/IIASA/ISRIC/ISSCAS/JRC, 2009).

Mean effects were estimated as the response ratio, which is the ratio of ANPP measured in experimental and control groups (relative yield). In comparisons across systems where response variables and experimental designs can differ considerably, the analysis of change relative to the control is more meaningful than standardized absolute differences between means (Hedges et al., 1999). We analyzed response ratios for all studies and for groups formed by the following categories: climate (arid: $0.05 < \text{MAP/PET} < 0.2$, semiarid: $0.2 < \text{MAP/PET} < 0.55$, and subhumid: $0.55 < \text{MAP/PET} < 0.75$, according to the MAP/PET ratio adapted from Le Houérou (1996)); natural vs. sown pastures systems; life form of dominant species (grass, shrub, forbs, or combinations of them); precipitation seasonality (concentrated in summer, winter or evenly distributed); and fertilizer form (NH_4NO_3, urea, ammonium sulphate or calcium nitrate).

Changes in mean effects along the following continuous variables were also estimated: MAP (mm yr^{-1}) and precipitation in the year of the experiment; mean annual temperature (°C); MAP/PET ratio; latitude; rate of N addition (g N m^{-2} yr^{-1}); and several soil characteristics. The complete list of studies included and characteristics are listed in Supporting Information.

2.2. Statistical analyses

We estimated the effect of N fertilization on ANPP as the response ratio (*R*), the ratio between ANPP estimated in the fertilized and control plots (Hedges et al., 1999). We then calculated the natural log of *R* from each study and analyzed data with the MetaWin Version 2.1 software (Rosenberg et al., 2000). We combined results from independent studies in a meta-analysis to test the overall response using a weighted-mixed effect model. Then, we included categorical effects such as vegetation dominant life form, precipitation seasonality, and fertilizer forms using a mixed-effects model. We calculated statistic Q_T to assess homogeneity of effect sizes. A significant Q_T indicates that the variance among effect sizes is greater than expected by sampling error and implies that other explanatory variable should be investigated (Hedges et al., 1999). For continuous variables, we estimated regression coefficients, the variance accounted for by the regression model (Qw), and the total variance among studies included in the regression that is used to assess homogeneity of effect sizes (Q_T).

We tested for publication bias, which is the selective publication of articles showing only certain type of results (Begg, 1994), and for normality with normal quantile plot and rank correlation. The test indicated no publication bias (Kendall'tau and Sperman's rho were −0.088 and −0.125 respectively, $P = 0.24$). In fact, the bias is minimized when the result of interest is part of a larger investigation because there is less chance that preferential publication of significant results occurs (LeBauer and Treseder, 2008). In the present analysis, several studies reported data from multiple rates of N addition, combination of phosphorus or water addition along with N addition, and/or multiple years of fertilization addition that certainly minimized publication bias for the subset of results analyzed.

3. Results

Our compilation of studies of fertilization in arid to subhumid ecosystems encompassed different biomes in four continents (Fig. 1), including 27 eco-regions according to classification by Olson et al. (2001) (Supporting Information). Nitrogen addition increased aboveground net primary production across all studies by 50% (Table 1). The fertilization effect was significant in arid, semiarid and subhumid ecosystems; and caused a 30%, 53%, and 60% increase in aboveground net primary production relative to controls, respectively. Only six out of the 68 cases showed lower or equal aboveground net primary production in fertilized than control plots (Fig. 2).

N fertilization effects on above ground net primary production increased significantly ($P = 0.03$) along the 50–650 mm yr^{-1} precipitation gradient (Fig. 3). Significant regressions were observed between R and mean annual precipitation (MAP) of the site and between R and precipitation during the year of the experiment (Table 2). The aridity gradient depicted by the MAP/PET ratio showed a significant ($P = 0.048$) effect on N fertilization responses, as nitrogen effects increased with increases in the MAP/PET ratio (Table 2). By contrast, the response ratio did not change significantly with latitude ($P = 0.51$) (Table 2). In addition, seasonal distribution of annual precipitation affected response ratios as ecosystems with summer or evenly distributed precipitation during the year showed significantly ($P = 0.03$) higher responses to N fertilization than ecosystems with predominantly winter precipitation (Table 1).

Across all studies, the regression between R and mean annual temperature (MAT) for the range 2–26.7 °C was not significant ($P = 0.45$) (Fig. 4). However, when studies from subhumid ecosystems (MAP higher than 400 mm yr^{-1} or MAP/PET higher than 0.55) were excluded, the response ratio significantly ($P = 0.023$) decreased with mean annual temperature (Table 2).

Pastures sowed with grasses showed significantly higher ($P = 0.007$) responses than natural ecosystems (Table 1). Within natural ecosystems, plant life forms did not show a significant effect ($P = 0.11$) on the response ratio (Table 1). The chemical form of the applied fertilizer did not show a significant effect ($P = 0.40$) on the aboveground net primary production response to N addition (Table 1). Nitrogen added as ammonium nitrate, which was the predominant N form used in published studies, produced a similar response ratio as the experiments fertilized with urea, ammonium–sulfate or calcium–nitrate. Response ratios increased with fertilization doses along the fertilization gradient employed, but the relationship was not significant ($P = 0.14$) (Table 2). Levels of fertilization among studies ranged from 2 to 100 g N m^{-2} yr^{-1} and they were not related to mean annual precipitation of the site ($P > 0.05$). The soil variables that we evaluated (texture as sand, silt and clay percentage, pH, organic carbon content, cation exchange capacity, sodicity, salinity, and water storage capacity) did not show an effect on the response ratio (data not shown).

4. Discussion

Nitrogen limits aboveground net primary production in most low-precipitation ecosystems as shown by an overall significant increase in ANPP with N fertilization. To our knowledge, this is the first clear evidence of widespread nitrogen limitation across arid to

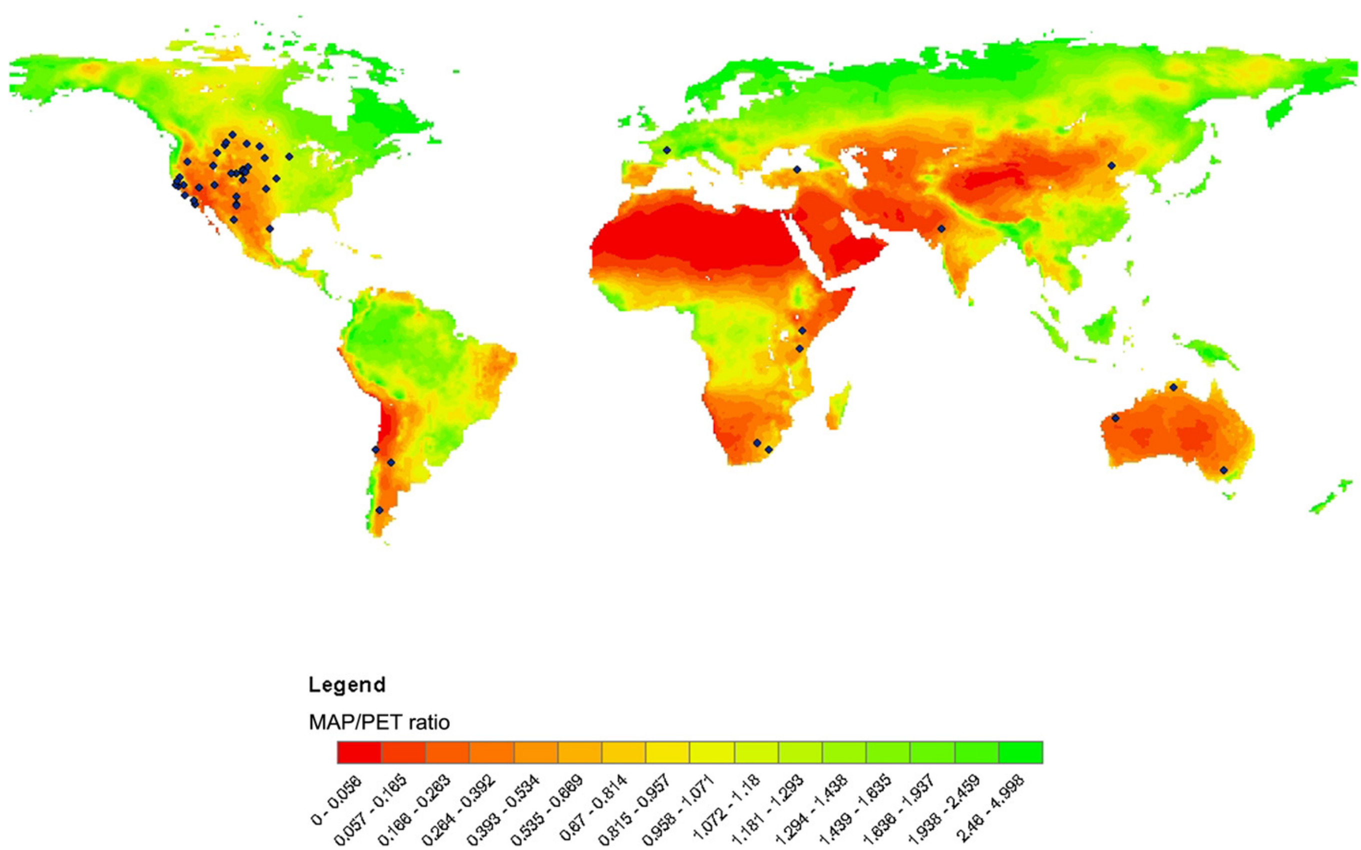

Fig. 1. Location of studies included in the meta-analysis and the Mean Annual Precipitation: Potential Evapotranspiration (MAP/PET) ratio. MAP/PET ratios were calculated with Worldclim database version 1.4 eighth with ArcGIS Desktop 9.2.

Table 1
Effects of nitrogen fertilization on aboveground net primary productivity (ANPP) in arid-subhumid ecosystems. Response ratios are presented overall and grouped by sown pastures versus natural systems, dominant vegetation life forms, precipitation seasonality, and fertilizer chemical forms. The response ratio, *R*, is the ratio of estimated ANPP in the fertilized to the control plots. An $R > 1$ reflects a positive ANPP response to nitrogen fertilization and indicates nitrogen limitation, which was statistically significant when the confidence interval did not include 1. The homogeneity statistic Q_T is used to assess homogeneity of effect sizes. Boldface type indicates responses that are significant at $P < 0.05$.

Grouping	N	R	95% CI	Q_T	P
Overall	68	1.51	1.42 to 1.60	60.55	
Sown pastures vs. natural	68			14.51	**0.007**
Natural	48	1.41	1.32 to 1.51		
Sown pastures	20	1.83	1.62 to 2.08		
Life forms within natural	48			6.28	0.11
Grasses	26	1.55	1.39 to 1.75		
Grasses and forbs	4	1.44	0.91 to 2.28		
Grasses and shrubs	16	1.25	1.09 to 1.44		
Shrubs	2	1.55	1.23 to 1.95		
Precipitation seasonality	68			12.61	**0.031**
Summer	40	1.56	1.45 to 1.67		
Winter	16	1.24	1.09 to 1.41		
Even	12	1.62	1.40 to 1.87		
Fertilizer forms	68			3.68	0.40
Ammonium nitrate	48	1.50	1.41 to 1.60		
Urea	13	1.40	1.20 to 1.64		
Ammonium sulfate	4	1.88	1.05 to 3.37		
Calcium nitrate	3	1.27	0.49 to 3.29		

subhumid ecosystems. Aboveground net primary productivity increased, on average, 51% as a result of N fertilization. This fertilization effect was comparable to those reported for temperate grasslands (53%) and tropical forests (60%) (LeBauer and Treseder, 2008). Our results support the conclusions of LeBauer and Treseder (2008) that nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. However, contrary to previous results which concluded that arid ecosystems were not limited by N (LeBauer and Treseder, 2008), we found that arid ecosystems that include desert biomes are also N limited. In addition, Elser et al. (2007) stated that freshwater, marine and terrestrial ecosystems (including only 3 sites below 650 mm MAP) are similar in terms of N limitations; and now we can reaffirm Elser's statement including arid and semiarid ecosystems to previously evaluated terrestrial ecosystems.

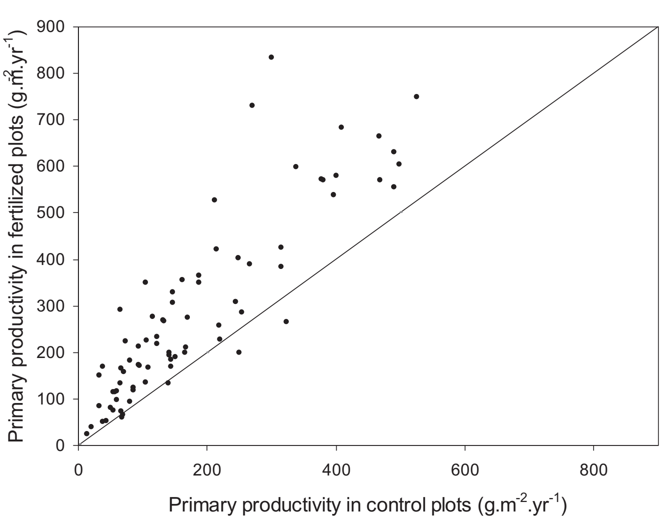

Fig. 2. The effect of N fertilization on aboveground net primary productivity in arid to subhumid ecosystems. Each data point represents a single comparison between fertilized and control treatments for a given field experiment ($n = 68$). Values falling on the 1:1 line indicate no response to N fertilization treatment; points above the line indicate ANPP stimulation after N fertilization, whereas points below indicate lower ANPP in fertilized than control plots.

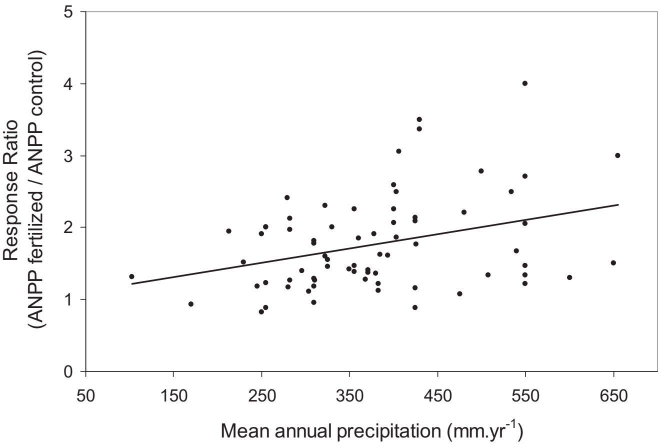

Fig. 3. The effect of fertilization on aboveground net primary production, estimated by the response ratio *R* (ratio of production in fertilized to control plots), in arid-subhumid ecosystems as a function of mean annual precipitation ($n = 68$). Ecosystem response to fertilization increased with precipitation as: $y = 0.003 \times + 0.83$; $r^2 = 0.20$; $P = 0.03$.

We found that along the arid to subhumid gradient, the fertilization effect on ANPP increased significantly. This pattern occurred when we looked at ecosystem response as a function of mean annual precipitation, precipitation during the year of the study, and water availability depicted by the MAP/PET ratio, which also takes into account differences in evaporative demand. The balance between water and N limitation in these systems is probably the result of the frequency (for example number of days per year) of limitation of each resource. Water is usually available as discrete precipitation pulses separated by dry periods. During precipitation and probably several days after rain events, soil water content increases and water becomes available for plant growth. During those moist periods, N limitation may be important. As the soil dries and water becomes less available for plants, N limitation may decrease in importance and water limitation would increase in significance. So, the balance of water versus N limitation is probably determined by the frequency of precipitation pulses, along with soil characteristics that determine water storage in the soil profile and the capacity of plants to use water at low water potentials. In synthesis, along the precipitation gradient, the fertilization

Table 2
Regressions between the response ratio (*R*) and environmental variables (precipitation, mean annual temperature, and MAP/PET ratio), latitude, and N fertilizer doses. Slopes of regressions are *R* vs. independent variables; *R* is the ratio of estimated aboveground net primary productivity in the fertilized to the control plots. Qw is the variance accounted for by the regression model; Q_T is the total variance among studies included in the regression that is used to assess homogeneity of effect sizes. Boldface type indicates regressions that are significant at $P < 0.05$.

Grouping	N	Slope	Qw	Q_T	P
Precipitation (mm yr^{-1})					
Mean annual precipitation	68	0.0030	6.41	59.96	**0.030**
Precipitation in the year of the experiment	68	0.0008	3.98	61.58	**0.040**
Mean annual temperature (°C)					
Overall	68	0.0063	0.57	120.53	0.450
Excluding subhumid	44	−0.016	7.93	90.80	**0.023**
MAP/PET	68	0.430	3.88	87.33	**0.048**
Latitude (*degree latitude*)	68	−0.0002	0.42	129.04	0.510
Fertilizer doses (g N m^{-2} yr^{-1})	68	0.0018	2.14	57.28	0.140

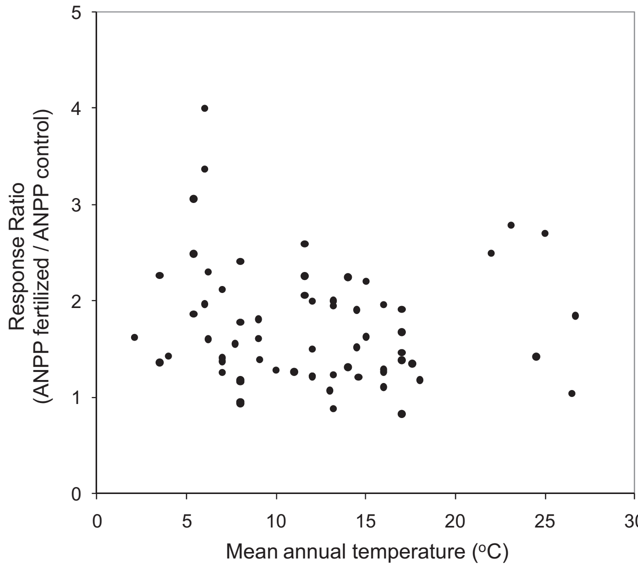

Fig. 4. The effect of fertilization on aboveground net primary production, estimated by the response ratio *R* (ratio of production in fertilized to control plots) in arid-subhumid ecosystems as a function mean annual temperature gradient ($n = 68$). Ecosystem response to fertilization was not related with mean annual temperature of the site ($r^2 = 0.004$; $P = 0.45$).

response increases probably because N limits more frequently ANPP and water availability less frequently, which occurs in subhumid climates. In addition, subhumid communities have a higher proportion of species with high relative growth rate, which result in a higher capacity to respond to increases in N availability, than communities in arid or semiarid ecosystems (Lambers and Poorter, 1992). Another explanation of the observed increase in the effect of N fertilization with increasing precipitation may be associated with the distribution of precipitation event sizes along the arid-subhumid precipitation range. The proportion of small rainfall events decreases with increasing annual precipitation (Lauenroth and Bradford, 2009). Theoretical and empirical studies indicated that small rainfall events have a larger effect per unit of precipitation on nitrogen mineralization than large events (Yahdjian and Sala, 2010) and the opposite would be true for plant growth and nitrogen absorption (Sala and Lauenroth, 1982). Therefore, as the frequency of small events decreases there would be a decrease in the short-term mineralization/immobilization ratio. So not only the frequency of water limitation but the decrease in the proportion of small events may increase N limitation with increasing precipitation.

Our results of no temperature effect on ecosystem responses to N fertilization agree with Hooper and Johnson (1999) and LeBauer and Treseder (2008). Only when subhumid studies were excluded from our database, *R* decreased with MAT for arid and semiarid ecosystems (MAP lower than 400 mm yr^{-1}). The increased temperature might exacerbate water limitation and, as we explained above, the N limitation decreases as the water limitation increases.

Ecosystems with summer or evenly distributed precipitation along the year showed higher ANPP responses to N fertilization than ecosystems where precipitation is concentrated during the winter. This is probably a consequence of more effective precipitation for plant growth when precipitation occurs during the time of the year with higher temperatures (growing season). Those times of the year when temperature and water availability are high are probably when frequency of N limitation is maximal.

Sowed pastures had higher responses to N fertilization than ecosystems dominated by natural vegetation. This is probably the result of pastures being dominated by plant species with high relative growth rate, which were selected to grow in sown pastures systems and under high fertilization conditions. Natural ecosystems dominated by grasses or shrubs or codominated by grasses and shrubs or grasses and forbs did not differ significantly in their response ratio. Even so, there was a bias in the data set toward studies performed in natural communities dominated by grasses. These results should be taken with caution as they were developed from only 2 cases dominated by shrubs and 4 codominated by grasses and forbs.

The response ratio did not change with chemical N forms of fertilizer used or with fertilizer doses applied. The majority of the studies included, 48 out of 68, reported experiments fertilized with ammonium nitrate, 13 were fertilized with urea, and very few experiments fertilized with other chemical forms such as calcium nitrate or ammonium sulfate. These findings are in agreement with previous meta-analysis of N fertilization experiments indicating that the chemical form employed did not influence primary production response ratio (see for example (LeBauer and Treseder, 2008). Our finding that there was not a significant effect of fertilizer dose on the productivity is similar to response reported by Hooper and Johnson (1999) who did not find a significant increase in aboveground primary productivity to fertilizer doses among ecosystems in the more arid extreme of the gradient (200–300 mm MAP). However within the 300–450 mm of MAP they did find a correlation of N response and fertilizer doses (Hooper and Johnson, 1999).

The results of the present study have implications for understanding ecosystem responses to future increases in N deposition rates as predicted by global change scenarios (Galloway and Cowling, 2002; Galloway et al., 2004). There is great interest in determining ecosystem responses to N deposition in arid and semiarid ecosystems because they occupy 40% of the terrestrial surface. Although arid lands have, in general, low rates of N deposition, long-term trends in some arid regions, like the northern Chihuahuan Desert of Central New Mexico in USA, showed N deposition increasing at an annual rate of 0.05 kg ha^{-1} yr^{-1} for the last 20 years (Báez et al., 2007). Our results indicate that N deposition would significantly increase aboveground net primary production and that increase will be larger in subhumid than in arid ecosystems.

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Appendix. Supplementary data

Supplementary data associated with the article can be found in online version, at doi:10.1016/j.jaridenv.2011.03.003.

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