LETTERS

Nitrogen limitation constrains sustainability of ecosystem response to CO_2

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Enhanced plant biomass accumulation in response to elevated atmospheric CO_2 concentration could dampen the future rate of increase in CO_2 levels and associated climate warming. However, it is unknown whether CO_2-induced stimulation of plant growth and biomass accumulation will be sustained or whether limited nitrogen (N) availability constrains greater plant growth in a CO_2-enriched world[1–9]. Here we show, after a six-year field study of perennial grassland species grown under ambient and elevated levels of CO_2 and N, that low availability of N progressively suppresses the positive response of plant biomass to elevated CO_2. Initially, the stimulation of total plant biomass by elevated CO_2 was no greater at enriched than at ambient N supply. After four to six years, however, elevated CO_2 stimulated plant biomass much less under ambient than enriched N supply. This response was consistent with the temporally divergent effects of elevated CO_2 on soil and plant N dynamics at differing levels of N supply. Our results indicate that variability in availability of soil N and deposition of atmospheric N are both likely to influence the response of plant biomass accumulation to elevated atmospheric CO_2. Given that limitations to productivity resulting from the insufficient availability of N are widespread in both unmanaged and managed vegetation[5,7–9], soil N supply is probably an important constraint on global terrestrial responses to elevated CO_2.

Continued emissions of CO_2 by the burning of fossil fuel are expected to increase global atmospheric CO_2 concentrations and surface temperatures significantly[1]. These changes will occur much more rapidly if the terrestrial or oceanic carbon sinks weaken in the future. However, predicting future atmospheric CO_2 concentrations is hampered by uncertainties surrounding biospheric responses to elevated CO_2, such as the possibility that soil N availability restricts the magnitude of CO_2-induced biomass enhancement[4–8]. However, the importance of, and the mechanisms underlying, this limitation to the CO_2 fertilization effect is a matter of debate[2,3,7,8,10–12]. This is not surprising, because even with widespread N limitation of net primary production in terrestrial ecosystems[13], the nature, timing and predictability of N constraints on ecosystem C accumulation remain unclear[2,6,8,11].

Multiple-resource-limitation theory provides a variety of mechanisms by which low N availability potentially limits the enhancement of biomass accumulation in response to elevated CO_2, but not all models agree that this will occur[2,3,10,14,15]. At elevated CO_2, low supply of N in the soil could limit the leaf area for intercepting light, limit the capacity of plants to fix CO_2 photosynthetically, or lead to diminishing plant N availability over time through long-term soil–plant C and N dynamics[2–4,8,11,15,16]. Each of these, or their combination, could diminish biomass response to elevated CO_2. Therefore,

a large increase in biomass accumulation under elevated CO_2, often observed in short-term experiments, may not be sustained over the long term in natural systems given the N limiting conditions that predominate in both unmanaged and managed vegetation[5,7,8].

Much research has addressed the response of N availability to elevated CO_2, but findings have been inconsistent. Soil N availability has been observed to decrease under elevated CO_2, but it has also been observed to remain stable or increase[8,12,16–19]. Moreover, results from studies that manipulated both CO_2 and N are variable in terms of whether biomass accrual under elevated CO_2 is affected by N supply[5,6,9,18,20–22]. The inconsistency of such responses may reflect inconsistent responses of soil N availability to elevated CO_2, but additionally they may reflect variation in nutrient-use efficiency, stoichiometry or soil microbial processes that may eliminate or delay the impact of N limitation on the elevated CO_2 response[2,8,12].

Most experiments that have manipulated CO_2 and N[5,6,18,20–22] have been short in duration (3 years or less), which limits their utility in understanding interactions that are predicted to occur over longer time frames[2,3,8,15]. Despite the importance of understanding $CO_2 \times N$ interactions, to our knowledge there are only three replicated field experiments in the world that have manipulated both CO_2 and N supply for more than three years (including ours reported here). Two of these experiments are relevant to natural systems (early results are reported in refs 6, 23) and one to intensively managed agricultural systems (long-term results are reported in ref. 9). In our experiment (called BioCON) we grew 296 field plots containing different numbers (1, 4, 9 or 16 species) and combinations of perennial grassland species under ambient and elevated (560 μmol mol^{-1}) atmospheric CO_2 and with either ambient or enriched soil N supply (ambient and enriched with 4 g N m^{-2} yr^{-1} as NH_4NO_3). A total of 16 native or naturalized species were used in the study, four each from four functional groups (legumes, non-leguminous forbs, C_3 grasses and C_4 grasses). The main effects of diversity and interactions with CO_2 and N were addressed previously[18,23]. We proposed that biomass accumulation of plants growing in ambient, N-poor soil would be less responsive to elevated CO_2 than would biomass of plants grown in N-enriched soil. The contrasting high versus low levels of N supply in our study are broadly consistent with the global range in both rates of N supply in unfertilized soils and in annual N deposition[13,24].

During the six years of the study, the stimulation of plant biomass accumulation by elevated CO_2 became continuously weaker under ambient N supply than under enriched N supply (Fig. 1). Both CO_2 and N generally stimulated biomass accumulation (Fig. 1, Table 1), and overall biomass levels declined after the first year and then varied over time. However, for the entire period there was a significant

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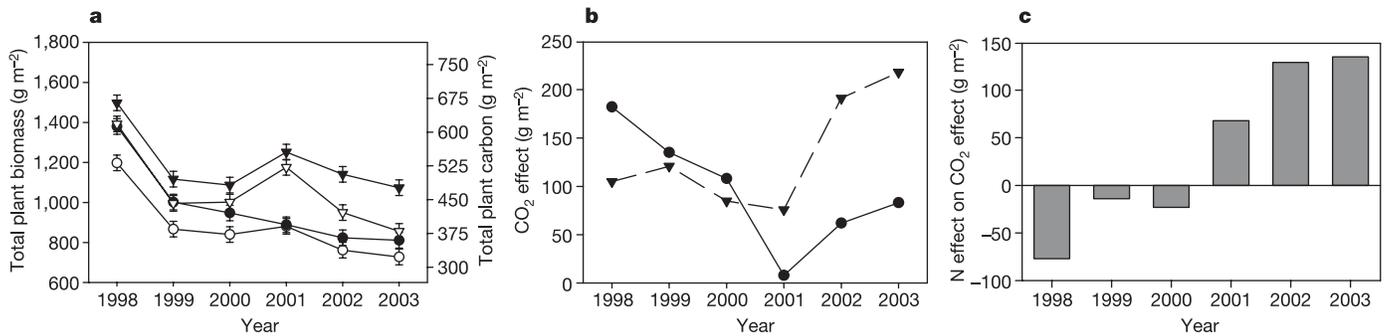
Figure 1 | Effects of CO$_2$ and N on total plant biomass over time. a, Total plant biomass (above-ground plus 0–20 cm below-ground) and carbon at ambient and elevated CO$_2$ × N levels from 1998 to 2003. Data were pooled across diversity treatments, and each point shows the annual mean (plus standard error) of 74 plots sampled twice per year. There was a significant interaction (Table 1) between CO$_2$, N and year ($P = 0.0013$), plus significant main effects ($P < 0.05$) of year, CO$_2$ and N. Open circles, ambient CO$_2$ and ambient N; filled circles, elevated CO$_2$ and ambient N; open triangles, ambient CO$_2$ and enriched N; filled triangles, elevated CO$_2$ and enriched N. **b**, The effect of CO$_2$ on total biomass: the CO$_2$ enhancement (assessed as (value at elevated CO$_2$) minus (value at ambient CO$_2$)) at ambient (circles) and enriched (triangles) N supply each year. **c**, The effect of N availability on the CO$_2$ biomass effect, defined as the difference between the CO$_2$ effect at enriched N and that at ambient N, namely (CO$_2$ effect at enriched N) minus (CO$_2$ effect at ambient N).

temporal shift in the enhancement of total biomass by CO$_2$ at ambient versus enriched N ($P = 0.0013$ for the CO$_2$ × N × year interaction; Table 1, Fig. 1). This impact over time of N supply rate on response to elevated CO$_2$ did not vary significantly with species diversity treatment. Data are therefore shown pooled across all species richness levels.

The significant three-way interaction involving CO$_2$, N and year occurred because the influence of enriched N supply on the CO$_2$ response shifted in direction and grew larger with time (Fig. 1b, c, Table 1). The stimulation of total biomass by elevated CO$_2$ was higher at ambient N than at enriched N each year from 1998 to 2000 (Fig. 1b), although for each year analysed individually there was no significant effect of N on the elevated CO$_2$ response. However, in 2001, 2002 and 2003 the sign of the CO$_2$ × N interaction switched: stimulation of total biomass by CO$_2$ was greater at enriched N supply than at ambient N supply (statistically significant CO$_2$ × N interaction in 2002 and 2003; $P < 0.05$). For example, in 2002 and 2003, respectively, elevated CO$_2$ increased biomass by 62 and 82 g m^{-2} at ambient N and by 191 and 219 g m^{-2} at enriched N (Fig. 1b). These correspond to 20–25% stimulation of biomass by elevated CO$_2$ at enriched N, compared with 8–12% stimulation at ambient N.

The mechanisms responsible for the changes with time in the response of biomass accumulation to CO$_2$ and N supply (Fig. 1) probably involve temporal heterogeneity in physiological acclimation, soil C and N mineralization and immobilization, and litter, root and soil organic matter decomposition and turnover[12,18,25–28]. For example, there were temporal changes in CO$_2$ × N effects on total plant N pools and on net N mineralization rates in soil, including significant ($P < 0.05$) interactions between CO$_2$, N and year in both cases (Table 1). These were a consequence of elevated CO$_2$ substantially increasing plant N pools and soil net N mineralization rates at enriched N supply in 2002 and 2003 (Supplementary Figs 1 and 2). These biomass and N cycle shifts in CO$_2$ × N response over time could result in part from the immobilization of N into living tissues (below-ground turnover is about three years) and decomposing organic matter. Such N sequestration would probably have been enhanced in the treatment with elevated relative to ambient CO$_2$ in the first two years of the study, because of higher biomass, initially higher biomass C:N ratios, and greater labile C inputs[28]. The positive response to CO$_2$ enrichment observed under ambient N during the first two years of the experiment may also be more characteristic of seedlings or juvenile plants than of mature, well-established plants.

Additionally, to test whether the accumulation of greater plant biomass at elevated CO$_2$ than at ambient CO$_2$ was due to a greater efficiency of use of N pools in C acquisition and accumulation, or to greater N pools, we examined the relationship between total plant biomass and total plant N across all plots. The slope of this relationship was greater at elevated CO$_2$ than at ambient CO$_2$ in 1998 and 1999 but not in 2000–2003 (Supplementary Table 1 and Supplementary Fig. 3; CO$_2$ treatment × plant N pool × year interaction, $P < 0.0001$). In 1998–1999, total plant biomass was about 15% higher at any given plant N pool at elevated CO$_2$ than at ambient CO$_2$. This CO$_2$-enhanced N use efficiency disappeared with time: from 2000 to 2003 plots with elevated CO$_2$ tended to occupy positions higher up on the same biomass–N relationship. These results indicate that in 1998–1999, stimulation of biomass accumulation by elevated CO$_2$ might have been related to increased efficiency of physiological N use, whereas in later years the CO$_2$ stimulation of biomass was associated with shifts in total plant N availability and accumulation.

We conclude from the results of our study that long-term biomass accumulation was influenced by the relative availability of CO$_2$ and N, with ambient N supply gradually limiting the potential biomass accumulation in response to elevated CO$_2$, and enriched N supply gradually stimulating this response. These responses were similar for simple monocultures and complex mixtures. Moreover, even the plots with legumes, generally considered responsive to elevated CO$_2$ independently of N supply[26,29,30], did not respond differently in terms of CO$_2$ × N interactions than plots without legumes. In separate analyses of variance there was no significant interaction of CO$_2$ × N × year with the presence or abundance of legumes or *Lupinus* (the most abundant legume) (Supplementary Table 2). Thus, the presence of legumes did not prevent the gradual development of a diminished elevated CO$_2$ biomass response at ambient N[30].

Our results are consistent with and extend previous experimental studies of CO$_2$ × N interactions in agricultural and forest plantation systems[5,9]. With its wide range of species types and species combinations, including mixtures, our study provides a broad test of CO$_2$ × N interactions under contrasting but relatively low N supply rates, and includes measurements of root biomass, whereas previous studies have been in a limited range of species monocultures with higher rates of N addition, and included no below-ground biomass measures[5,9]. In a two-year manipulation of CO$_2$ × N in a 15-year-old pine plantation, wood production increased with elevated CO$_2$ with a N addition of 11 g N m^{-2} yr^{-1} but not under ambient N conditions[5]. In a long-term study in a highly managed pasture[9], harvestable above-ground biomass in *Lolium* monocultures increased by more than 150 g m^{-2} yr^{-1} with elevated CO$_2$ when N addition was 56 g N m^{-2} yr^{-1} but did not increase when N addition was 14 g N m^{-2} yr^{-1}.

Table 1 | Repeated-measures analysis of variance of CO_2 and N effects

Effect	Total biomass ($g\,m^{-2}$)		Total plant N ($g\,m^{-2}$)		Net soil N mineralization ($mg\,kg^{-1}\,d^{-1}$)	
	F	P > F	F	P > F	F	P > F
CO_2	**11.17**	**0.0288**	52.95	0.1609	0.01	0.9303
N	**46.77**	**<0.0001**	77.90	**<0.0001**	1.55	0.2141
Year	**471.52**	**<0.0001**	1.87	0.1714	**7.06**	**0.0080**
$CO_2 \times$ year	0.01	0.9283	**11.68**	**0.0006**	3.64	0.0566
N $\times$ year	**9.84**	**0.0017**	1.46	0.2264	1.23	0.2671
$CO_2 \times$ N	0.38	0.5356	0.01	0.9196	1.10	0.2963
$CO_2 \times$ N $\times$ year	**10.35**	**0.0013**	**3.86**	**0.0497**	**4.25**	**0.0394**
Diversity	**133.25**	**<0.0001**	75.57	**<0.0001**	16.21	**<0.0001**
Whole-model R^2	**0.58**	**<0.0001**	0.40	**<0.0001**	0.21	**<0.0001**

Effects of year, CO_2, N and diversity, and all interactions, on total biomass (above-ground plus 0–20 cm below-ground), total plant N per unit ground area, and net soil N mineralization rate are shown. Year is included in the model as a continuous variable. Diversity was a significant main effect in all analyses but it did not influence the $CO_2 \times$ N interaction ($CO_2 \times$ N $\times$ diversity, $P \geq 0.4$) or the year $\times CO_2 \times$ N interaction ($CO_2 \times$ N $\times$ year $\times$ diversity, $P \geq 0.4$). Interaction terms including diversity effects are therefore not shown above, and effects of year, CO_2 and N are shown pooled across diversity treatments in Fig. 1 and Supplementary Information. Significant effects ($P \leq 0.05$) are shown in bold text.

Findings from both of these studies are consistent with our results, indicating that the overarching control on responses to elevated CO_2 by C:N supply stoichiometry might be comparable in intensive agricultural, forest plantation and natural ecosystems, although the N levels required to alleviate N limitation in agricultural systems may be an order of magnitude higher than in unmanaged vegetation. Given that the levels in our N treatments (ambient and $+4\,g\,N\,m^{-2}\,yr^{-1}$), and their difference, were within the global range of variation of both natural soil N availability and of atmospheric N deposition[13,24], the results indicate that variabilities in soil N and in atmospheric N deposition are both likely to influence terrestrial ecosystem responses to elevated CO_2. In sites with low-to-moderate soil N availability, N limitation probably constrains the stimulation of biomass accumulation by elevated CO_2. In soils that are N-rich and in regions with very high levels of N deposition, such limitation of the CO_2 fertilization effect by insufficient N may be weak or absent.

Our results are consistent with the idea[7] that although some models indicate a considerable capacity of land ecosystems to sequester large amounts of C in the coming century[1], this C accumulation is likely to be constrained over time by N availability[7,8]. Moreover, predictions of global C and N dynamics, and policy and political decisions whose efficacy rests on such predictions, should incorporate the impacts of multiple global change factors such as anthropogenic fertilization with C and N, as well as the interactions between these and other global factors. Estimating the role of terrestrial ecosystems as current and future carbon sinks hinges on the ability to understand the biogeochemical consequences of variability in soil N limitations and N deposition rates worldwide.

METHODS

In our experiment (called BioCON) we grew 296 field plots (each $2\,m \times 2\,m$) containing different numbers and combinations of perennial grassland species under ambient and elevated atmospheric CO_2 and with either ambient or enriched soil N supply[18,25]. Plots were arranged in six circular 20-m diameter rings at the Cedar Creek Natural History Area in central Minnesota, USA. In three elevated-CO_2 rings, a free-air CO_2 enrichment system[18] was used during each growing season to maintain the CO_2 concentration at an average of $560\,\mu mol\,mol^{-1}$, a concentration likely to be reached this century. Three ambient CO_2 rings were treated identically but without additional CO_2. Half of the plots in each ring received N amendments of $4\,g\,N\,m^{-2}\,yr^{-1}$ applied as NH_4NO_3 on three dates each year. The treatments were arranged in complete factorial combination of two levels of atmospheric CO_2 (ambient and elevated), four levels of plant species richness (1, 4, 9 and 16) and two levels of N (ambient and enriched with added N) (see Supplementary Information and refs 18, 25 for

further detail). There were 32, 15, 15 and 12 plots with 1, 4, 9 and 16 species, respectively, at each of the four contrasting CO_2 and N levels ($n = 296$ plots in all). The 16 study species included four C_4 grasses (*Andropogon gerardii*, *Bouteloua gracilis*, *Schizachyrium scoparium* and *Sorghastrum nutans*), four C_3 grasses (*Agropyron repens*, *Bromus inermis*, *Koeleria cristata* and *Poa pratensis*), four N-fixing legumes (*Amorpha canescens*, *Lespedeza capitata*, *Lupinus perennis* and *Petalostemum villosum*) and four non-leguminous forb species (*Achillea millefolium*, *Anemone cylindrica*, *Asclepias tuberosa* and *Solidago rigida*).

Each year in every plot we assessed both above-ground and below-ground (0–20 cm) plant biomass (in both June and August) and plant C and N concentrations (in August only)[18,25]. Above-ground biomass was harvested by clipping a 10 cm × 100 cm strip just above the soil surface. Total below-ground biomass (fine roots, coarse roots and crowns) was sampled at 0–20 cm depth with the use of three cores 5 cm in diameter. Soil net N mineralization rates were measured *in situ* each year in each plot by using a semi-open core one-month incubation[18] beginning in late June. We examined results for the entire period 1998–2003 and used a repeated-measures analysis of variance to test for the main effects of CO_2, N and diversity and their interactions, and whether these changed with year.

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Author Contributions All authors were involved in the design or implementation of the experiment, or both, with P.B.R. having the major responsibility for these. P.B.R., D.E., D.T., J.K. and S.N. were involved in the initial experimental design. J.T. was responsible for a substantial fraction of the experimental management and data collection, with smaller contributions in this area from T.L., D.E., J.B.W., J.K. and S.H. P.B.R. performed the statistical analyses and wrote the paper, with assistance from S.H., T.L., D.E., S.N. and J.B.W. All authors discussed the results and commented on the manuscript.

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