

PLANT ECOLOGY

Unexpected reversal of C₃ versus C₄ grass response to elevated CO₂ during a 20-year field experiment

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Theory predicts and evidence shows that plant species that use the C₄ photosynthetic pathway (C₄ species) are less responsive to elevated carbon dioxide (eCO₂) than species that use only the C₃ pathway (C₃ species). We document a reversal from this expected C₃-C₄ contrast. Over the first 12 years of a 20-year free-air CO₂ enrichment experiment with 88 C₃ or C₄ grassland plots, we found that biomass was markedly enhanced at eCO₂ relative to ambient CO₂ in C₃ but not C₄ plots, as expected. During the subsequent 8 years, the pattern reversed: Biomass was markedly enhanced at eCO₂ relative to ambient CO₂ in C₄ but not C₃ plots. Soil net nitrogen mineralization rates, an index of soil nitrogen supply, exhibited a similar shift: eCO₂ first enhanced but later depressed rates in C₃ plots, with the opposite true in C₄ plots, partially explaining the reversal of the eCO₂ biomass response. These findings challenge the current C₃-C₄ eCO₂ paradigm and show that even the best-supported short-term drivers of plant response to global change might not predict long-term results.

The idea that C₄ plants are less limited by ambient atmospheric CO₂ concentrations than C₃ plants, and will thus respond less to increasing CO₂ concentrations, has a long history (1–3) and is deeply embedded in models of past, present, and future vegetation-climate interactions (2–7). The hypothesis has proven useful, if not always entirely predictive, in describing C₃ and C₄ plant distributions (2–4, 8–11) and biomass responses to environmental variation (12–15).

There is strong logic for this hypothesis. C₃ plants, which use the carboxylase enzyme RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) to fix CO₂ from the air and obtain 3-carbon intermediate molecules as the first step in photosynthesis, lose a portion of their fixed CO₂ to oxidative photorespiration under present CO₂:O₂ ratios because RuBisCO is also an oxygenase (1–3). Thus, C₃ plants should exhibit increased leaf-level net photosynthesis as increasing CO₂:O₂ ratios reduce rates of photorespiration and increase rates of carboxylation (1–3). By contrast, in C₄ plants, a different enzyme (phosphoenolpyruvate carboxylase) with a high affinity for CO₂ and lacking oxygenase activity first incorporates CO₂ into a 4-carbon intermediate, which is then shuttled to specialized bundle sheath cells where CO₂ is released, resulting in locally high CO₂ concentrations. Here, RuBisCO catalyzes carboxylation, but with low rates of photorespiration because of the high CO₂:O₂ ratios in the bundle sheath cells. As a result, eCO₂ levels in air have little impact on

photosynthetic rates for C₄ plants (1–3). Globally, most plants are C₃; graminoids are the only major group with substantial abundance of both C₃ and C₄ species (2, 16). Given that C₄ grasslands may constitute one-fifth of global terrestrial net primary productivity (16), a better understanding of C₄ performance under rising CO₂ vis-à-vis C₃ grasses is needed for global ecology and for improved ecosystem and Earth system modeling (5–7, 17). C₃ and C₄ grasses (and sedges) are also distinguished in terms of ecological success by different affinities for temperature, rainfall, and nutrient supply (as well as CO₂); as a consequence, they can co-occur or shift their relative abundances depending on the mix of conditions (8–11, 14, 15, 18–20).

Experimental evidence has strongly supported the theoretical prediction that at current CO₂ levels, C₃ grasses are more CO₂-limited than C₄ species and thus will respond more to rising CO₂. Two influential meta-analyses (12, 13) reported greater stimulation (by factors of 2 to 4) of above-ground biomass by eCO₂ for C₃ species than for C₄ species. One of those publications focused on published studies of graminoids, where plants were mostly grown in pots for less than a year (12), whereas the other focused on free-air CO₂ enrichment (FACE) field studies (mostly 3 years or shorter) with plants grown in the ground (13). Another more recent meta-analysis also showed much greater responses of biomass growth for C₃ than for C₄ plants (21). One of the few longer-term studies comparing C₃ and C₄ grasses under eCO₂ found that C₄ species were, surprisingly, apparent “winners” after 3 years of eCO₂ and warming (20). However, by 6 years of treatment, the situation had reversed, with C₃ species becoming more positively responsive to the simulated global changes and the dominant plant type, in accordance with expectations (22).

In sum, current physiological theory and short- and medium-term studies support the paradigm

that C₄ species benefit much less from rising CO₂ than C₃ species. Given both theoretical and empirical support for the differences in eCO₂ response of C₃ and C₄ species, their differential responsiveness to eCO₂ comes as close to “accepted fact” as exists in ecology and, as such, is incorporated into many ecosystem and Earth system models (3–6, 8–13). However, it is not known whether findings from short- and medium-term studies apply over ecologically realistic time frames (>10 years) in field settings where complex feedbacks might influence response to eCO₂. Understanding long-term responses of C₃ and C₄ species is especially germane given that the limited available evidence suggests strong nonlinearity of responses of ecosystems to eCO₂ over time (23).

Here, we report results from a long-term (20-year) FACE experiment in Minnesota, USA, that support the long-held paradigm for the early part of the experiment but reveal a gradual reversal to a much more positive response to eCO₂ by C₄ than by C₃ grasses. The study uses 88 plots that are components of several different but overlapping global change experiments within the BioCON project (24, 25) and by themselves constitute a fully factorial 2 × 2 × 2 × 2 experiment of CO₂ levels (ambient or +180 parts per million), nitrogen levels (ambient or +4 g N m⁻² year⁻¹), species richness (one or four species), and functional group identities (C₃ or C₄ grasses) (26). Eight species of temperate perennial grasses (four each of C₃ and C₄) were used in the study (26) and were equally weighted in the original plantings of those 88 plots; that is, there are equal numbers of replicated monocultures of all species, and the four-species plots contain all species within each functional group. Annually over 20 years, we sampled both above-ground and belowground (0 to 20 cm) biomass late in each growing season in every plot, and also made an independent measure of fine root production (0 to 20 cm). We also measured in situ soil net N mineralization in every plot for a 1-month period each year just prior to biomass sampling (26, 27). Leaf-level net photosynthetic rates were measured midseason (28) for a subset of these eight grass species in 16 of the 20 years.

Over the 20-year experimental period, total biomass of C₄ grasses became increasingly enhanced by eCO₂ exposure, with the reverse true for C₃ grasses (Figs. 1 and 2 and figs. S1 and S2). During approximately the first 12 years (1998–2009), results were as expected (Fig. 1): C₃ plots averaged a 20% increase in total biomass (+136 g/m²) at eCO₂ relative to ambient CO₂, in contrast to C₄ plots that averaged a 1% increase (+12 g/m²). During the subsequent 8 years (2010–2017), the pattern reversed: C₃ plots averaged 2% less (–12 g/m²) and C₄ plots 24% more (+233 g/m²) biomass in eCO₂ than in ambient CO₂ (Fig. 1).

Repeated-measures analyses of variance (Table 1) support these conclusions, which are illustrated for successive 5-year periods in Fig. 2. Significant main effects on total biomass were found for N addition (higher biomass than at ambient N), species richness (higher biomass in plots with four species than in plots with one species), and functional group (higher biomass on average in

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C₄ plots than in C₃ plots) (Table 1). Additionally, on average across treatments, biomass of C₃ plots was originally greater than that of C₄ plots, but over time this ranking reversed (interaction of functional group × year, $P < 0.0001$; Table 1 and Fig. 1). Most germane was the significant functional group × year × CO₂ interaction ($P = 0.007$; Table 1), showing that C₃ and C₄ functional groups responded differently to eCO₂ over time (Fig. 2). For example, in each of the first two 5-year periods, C₃ grasses increased biomass under eCO₂ by ~20% (+140 g/m²); this declined to a 10% enhancement (+40 g/m²) in years 11 to 15 and a 2% decline in years 16 to 20 (-15 g/m²). In contrast, under eCO₂, biomass of C₄ grasses was reduced by 2% (-23 g/m²) in years 1 to 5, enhanced by ~7% (+60 g/m²) in years 5 to 10 and 11 to 15, and enhanced by 31% (+298 g/m²) in years 16 to 20. These different responses of functional groups to CO₂ and time were unaffected by N treatment ($P = 0.76$ for functional group × year × CO₂ × N interaction) and were slightly more pronounced in four-species plots than in one-species plots ($P = 0.048$ for functional group × year × CO₂ × species richness interaction) (Table 1 and fig. S3). Results were generally similar for aboveground and belowground biomass viewed separately, as well as for annual net primary production (estimated as the sum of annual aboveground biomass production and fine root production).

We explored several potential mechanisms for this long-term reversal of C₃ versus C₄ responsiveness to eCO₂, including a temporal switch in leaf-level photosynthetic response, differential CO₂ sensitivity associated with potential climate variation over the 20 years, and potential feedbacks from changing N cycle responses to eCO₂ over time. Measurements of light-saturated net photosynthesis were made for one to three C₃ and one to three C₄ grass species (mean of 2.2) in monocultures in 16 of the 20 years of the study, at all combinations of CO₂ and N treatment. There was no evidence of a shift over time in the enhancement of net photosynthesis as observed for biomass (no interactions of functional group × CO₂ × year; fig. S4). Moreover, there was no correspondence between years when eCO₂ enhancement of net photosynthesis was high and years when eCO₂ enhancement of biomass was high, in either functional group (compare Fig. 1 and fig. S4). Although we lack data for all species in all treatments in all years, the available data provide no evidence to suggest that the rank reversals of biomass responses to eCO₂ were driven by parallel rank reversals in leaf-level photosynthetic responses.

We then asked whether the shifting responsiveness of C₃ versus C₄ grass plots could be related to interannual variation in temperature or rainfall (2–5, 15, 19, 21). Responses of C₃ and C₄ grasses did not depend on year-to-year variations in mean or lagged spring, summer, or growing-season daily average temperature. The only significant effect involved summer rainfall [May to July (MJJ)]: There was a significant ($P = 0.0264$) interaction of CO₂ × functional group × MJJ rain-

fall on the biomass response (table S1); C₄ grasses were slightly more responsive to eCO₂ when rainfall was higher, whereas C₃ grasses were more responsive in low rainfall. These results are inconsistent with C₃ and C₄ grass responses in many

studies (2–5, 15, 19). However, MJJ rainfall was only weakly correlated with year, and the CO₂ × year × functional group interaction was significant in the model ($P = 0.0347$) even after accounting for differential responses to rainfall for the two functional

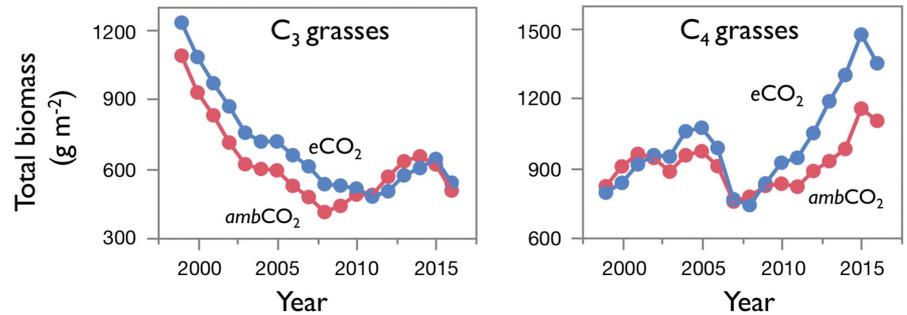


Fig. 1. Biomass over time of C₃ grasses and C₄ grasses at ambient and elevated CO₂. Total biomass (aboveground + 0 to 20 cm belowground) of plots comprising C₃ grasses and C₄ grasses in ambient CO₂ (red) and elevated CO₂ (blue) from 1998 to 2017. Data are shown as moving 3-year averages centered over the middle of each 3-year group. Each point represents data pooled across N treatments, and across monoculture and four-species plots (equally weighted), for each functional group ($n = 22$ plots for each functional group at each CO₂ level). See Table 1 for statistical analysis and fig. S1 for annual data and information on variation in response within treatments.

Table 1. Summary of repeated-measures analysis of variance of year, CO₂, N, species richness (SR), and C₃ versus C₄ functional group (FuncGroup) effects on total biomass and soil net N mineralization. Three-way or higher interactions involving treatments and two-way interactions or higher involving covariates shown only if significant. Five-way interactions were not tested. N mineralization data were missing for 2008 and 2017. Biomass was log-transformed prior to analysis. Year was a continuous term; Year and Year × Year terms were included in the model to assess linear and nonlinear changes over time involving CO₂ and functional groups. Significant terms ($P < 0.05$) in bold font.

Effect	Total biomass (g m ⁻²)		Net N mineralization (mg kg ⁻¹ day ⁻¹)	
	$R^2 = 0.609, P < 0.0001, n = 1760$		$R^2 = 0.086, P < 0.0001, n = 1582$	
Whole model	<i>F</i>	<i>P</i> > <i>F</i>	<i>F</i>	<i>P</i> > <i>F</i>
Year	158.95	<0.0001	0.31	0.5787
CO ₂	2.92	0.1521	0.75	0.4020
N	13.14	0.0005	12.19	0.0008
SR	10.11	0.0022	0.01	0.9187
FuncGroup	42.32	<0.0001	5.52	0.0195
Year × CO ₂	1.96	0.1614	0.39	0.5327
Year × N	2.26	0.1326	2.08	0.1493
Year × SR	23.64	<0.0001	0.00	0.96865
Year × FuncGroup	296.56	<0.0001	1.46	0.2269
CO ₂ × N	0.01	0.9342	0.67	0.4170
CO ₂ × SR	0.01	0.9265	0.36	0.5505
CO ₂ × FuncGroup	0.02	0.8965	0.49	0.4853
N × SR	1.42	0.2379	0.73	0.3953
N × FuncGroup	0.48	0.4885	5.48	0.0221
SR × FuncGroup	0.40	0.5314	0.56	0.4574
Year × CO ₂ × FuncGroup	7.24	0.0072	3.99	0.0461
Year × CO ₂ × FuncGroup × SR	3.89	0.0486	1.16	0.2827
Year × Year	104.34	<0.0001	20.87	<0.0001
Year × Year × CO ₂	0.23	0.6325	0.42	0.5189
Year × Year × CO ₂ × FuncGroup	0.08	0.7709	0.27	0.6034

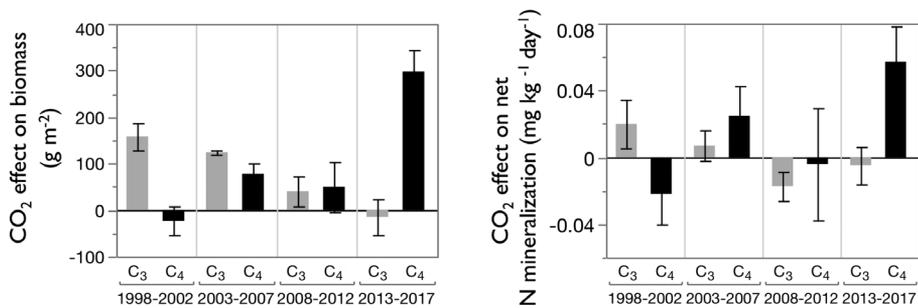
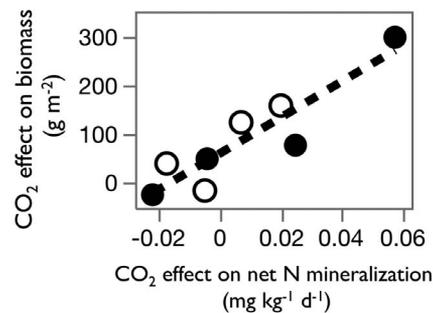


Fig. 2. Elevated CO₂ effect on total biomass and soil net N mineralization rates in plots comprising C₃ grasses and C₄ grasses. Left: Mean annual difference in biomass (mean biomass in eCO₂ – mean biomass in ambient CO₂) for C₃ and C₄ plots for four time periods during the study (1998–2002, 2003–2007, 2008–2012, and 2013–2017). Right: Mean difference in mean soil N mineralization rate (eCO₂ – ambient CO₂) for C₃ and C₄ plots for the same four time periods. Each bar represents data pooled across N treatments, and across monoculture and four-species plots (equally weighted), for each functional group ($n = 22$ plots for each functional group at each CO₂ level). Error bars represent SE among years.

Fig. 3. Correspondence between biomass and net N mineralization responses to elevated CO₂. Relationship of biomass response to eCO₂ (effect size = biomass in eCO₂ – biomass in ambient CO₂) versus net N mineralization response to eCO₂ (defined similarly) in plots comprising C₃ grasses (open circles) and C₄ grasses (solid circles). $R^2 = 0.82$, $P = 0.0018$. Each data point represents effect sizes for each functional group for the four 5-year periods during the study (as in Fig. 2), based on the average biomass and net N mineralization across years in each period at each CO₂ level.



groups by including rainfall and rainfall interactions in the model (table S1). Thus, the reversal of responsiveness of C₃ and C₄ plots to eCO₂ over time was not explained by interannual variation in precipitation.

We also considered soil processes that might have played a role in the shifting responses of the C₃ and C₄ assemblages. Soil N supply has shaped the dynamics of biomass response to eCO₂ in the wider BioCON experiment (including the 9- and 16-species mixtures) because, as predicted by multiple resource limitation theory, responses to eCO₂ were greater when N supply levels were high [e.g., (27)]. Hence, we asked what role soil N availability (using soil net N mineralization as an index) might play here. The response of soil net N mineralization to eCO₂ changed over time (Table 1, Fig. 2, and figs. S2 and S5), mirroring responses of biomass for the C₃ and C₄ groups (Table 1). There was a significant ($P = 0.046$) interaction of CO₂ × year × functional group: The response of net N mineralization to eCO₂ in C₄ grass plots became more positive over time, whereas that of C₃ grass plots became more negative (Table 1 and Fig. 2).

Moreover, relationships between biomass and soil net N mineralization rate, in concert with the shifts in the response of net N mineralization to eCO₂ over time, help to explain the shifting biomass response to eCO₂ of both functional groups. Biomass and its response to eCO₂ were both positively related to net N mineralization rate: Across years,

biomass in both functional groups increased with net N mineralization ($P = 0.0031$; table S1), more so at eCO₂ than at ambient CO₂ (interaction of CO₂ × net N mineralization, $P = 0.024$; table S1), and more so in C₄ than in C₃ plots (interaction of CO₂ × functional group, $P = 0.038$; table S1). Given that biomass is positively related to net N mineralization, and that the net N mineralization response to eCO₂ was increasingly positive over time in C₄ grass plots and increasingly negative in C₃ grass plots, shifting soil N biogeochemistry partially explains the shifting biomass responses to eCO₂.

These effects can be illustrated by the significant positive linear relationship between the eCO₂ enhancement of biomass and the eCO₂ enhancement of net N mineralization for the four 5-year periods of the study (Fig. 3): In periods when net N mineralization rates were higher under eCO₂ than under ambient CO₂, biomass tended to be higher in eCO₂ as well (Fig. 3 and table S1). These results are consistent with prior results showing that response to eCO₂ in this ecosystem is partially contingent on N supply (27), with greater N availability tending to promote greater eCO₂ response. Overall, 20 years of observations in this FACE experiment suggest that the opposite directional responses of net N mineralization to eCO₂ over time in C₃ versus C₄ grass plots (Table 1 and Fig. 2) may have contributed to the reversal of C₃ and C₄ biomass responses to eCO₂ over time. Why these soil N cycling responses played out in this fashion remains an open question, however.

Models that simulate future carbon cycling responses at ecosystem, regional, and global scales assume differing sensitivities of C₃ versus C₄ species to CO₂ based on differences in their photosynthetic physiology (5, 6, 8–11, 17). Although those assumptions have major impacts on vegetation dynamics under varying climate and CO₂ scenarios (8–11, 29, 30), they do not match up well with the dynamic results of this long-term study. Our results thus serve as a reminder that even the best-predicted short-term ecosystem responses to global change can yield mid-term (decades) to long-term (centuries) surprises, as complex responses and interactions may occur over time. Determining whether the mid- to long-term responses demonstrated here are themselves broadly predictable represents a major unmet challenge for experimental and observational studies.

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P.B.R. wrote the first draft; and all authors jointly revised the manuscript.
Competing interests: None. **Data and materials availability:** The data reported in this paper are available at the Environmental Data Initiative (EDI) (net nitrogen mineralization, DOI 10.6073/pasta/2ac4677a9292904628771d0df375ffa4; net nitrogen mineralization, DOI 10.6073/pasta/2ac4677a9292904628771d0df375ffa4; aboveground biomass, DOI 10.6073/pasta/8524be9f00b40a9e71b73a8ba2dc9ed0; belowground

biomass, DOI 10.6073/pasta/c00662959002e588597bd77e0c7dbdbb). All other data needed to evaluate the conclusions in the paper are present in the paper or the supplementary materials.

SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S5
Table S1
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A short-term trend reversed

Theory and empirical data both support the paradigm that C₄ plant species (in which the first product of carbon fixation is a four-carbon molecule) benefit less from rising carbon dioxide (CO₂) concentrations than C₃ species (in which the first product is a three-carbon molecule). This is because their different photosynthetic physiologies respond differently to atmospheric CO₂ concentrations. Reich *et al.* document a reversal of this pattern in a 20-year CO₂ enrichment experiment using grassland plots with each type of plant (see the Perspective by Hovenden and Newton). Over the first 12 years, biomass increased with elevated CO₂ in C₃ plots but not C₄ plots, as expected. But over the next 8 years, the pattern reversed: Biomass increased in C₄ plots but not C₃ plots. Thus, even the best-supported short-term drivers of plant response to global change might not predict long-term results.

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