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Grassland Responses to Global Environmental Changes Suppressed by Elevated CO_2

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Simulated global changes, including warming, increased precipitation, and nitrogen deposition, alone and in concert, increased net primary production (NPP) in the third year of ecosystem-scale manipulations in a California annual grassland. Elevated carbon dioxide also increased NPP, but only as a single-factor treatment. Across all multifactor manipulations, elevated carbon dioxide suppressed root allocation, decreasing the positive effects of increased temperature, precipitation, and nitrogen deposition on NPP. The NPP responses to interacting global changes differed greatly from simple combinations of single-factor responses. These findings indicate the importance of a multifactor experimental approach to understanding ecosystem responses to global change.

Human actions are affecting many aspects of the Earth system. The composition of the atmosphere, the climate, the abundance of invasive species, and the area of managed landscapes have all undergone important changes in the past century. These changes are likely to be even greater in this century (*1*). In almost any setting, realistic global change is decidedly multifactorial. Warming, increased precipitation, increased deposition of N-containing compounds, and increased atmospheric CO_2 are all likely consequences of CO_2 emissions from fossil fuel combustion and land use change (*2*). In the past century, atmospheric CO_2 concentration has increased globally by more than 30% (*2*). Temperature, precipitation, and deposition of biologically available N have increased for large regions (*3–5*). Further increases in the future are almost certain.

Most of the experimental research on ecosystem responses to global change has addressed responses to single global changes, with relatively few studies exploring responses to two or more interacting treatments (*6–8*). Experimental manipulations of both temperature and CO_2 concentration are rare at the ecosystem scale (*9*, *10*), even though elevated CO_2 is a primary driver of climate change (*2*).

Several modeling studies have addressed ecosystem responses to multifactor global changes (*11*, *12*), but the theoretical foundation for predicting ecosystem responses to simultaneous changes in multiple factors is incomplete. For some processes (such as photosynthesis), well-tested mechanistic models support the simulation and interpretation of multifactor responses (*13*). For many other processes, however, including biomass allocation, the timing of seasonal activity, and species replacements, the empirical data are too sparse to support credible models or allow comprehensive hypothesis tests.

Both empirical and modeling studies highlight potential contrasts in responses to single global changes and multiple, interacting global changes. Stimulation of plant growth by elevated CO_2, for example, may be strongest when water is limiting (*14*), when nutrients are abundant (*15*), or when plant species diversity is high (*6*). Simulated ecosystem responses to future global changes depend strongly on such interactions. In many settings, simulated warming increases decomposition more than net primary production (NPP), leading to a loss of carbon (*16*). In others, elevated CO_2 and N deposition tend to increase NPP more than decomposition, leading to carbon storage. In some simulations, the responses of carbon storage to the three factors nearly cancel one another out. In others, changes combine in nonadditive ways, with examples of both suppression and amplification (*11*).

One of the keys to understanding the long-term impacts of multiple global changes on ecosystem function will be experiments on model ecosystems that are amenable to factorial manipulations and respond rapidly. Annual grassland, with a high diversity of small short-lived plants, is an attractive model system for global change experiments. An area of less than 1 m^2 is sufficient for a meaningful global-

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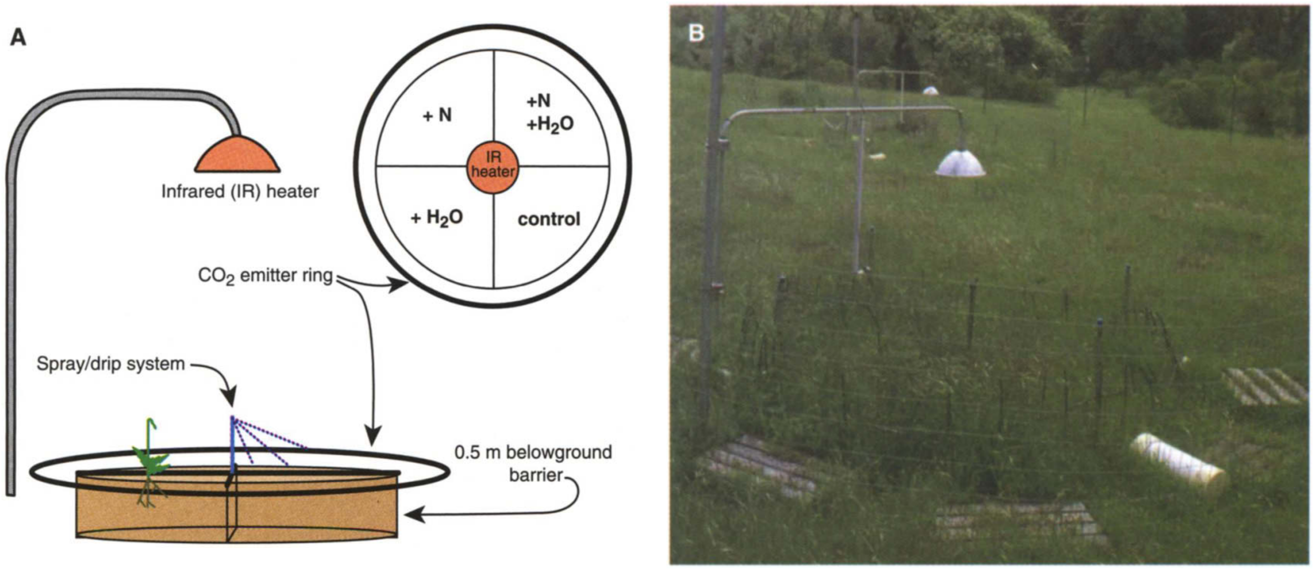

Fig. 1. (**A**) Schematic drawing of the study plots, side view (left) and top view (right). The plot is 2 m in diameter. (**B**) Photograph of a study plot.

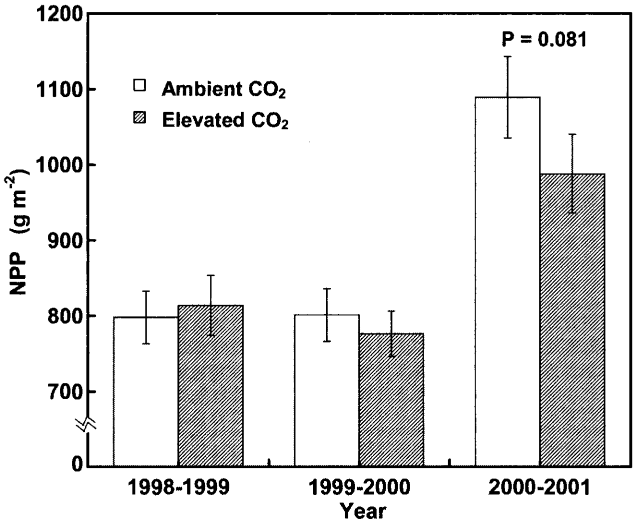

Fig. 2. NPP. Open bars represent all treatment combinations with ambient CO_2. Gray bars represent all treatment combinations with elevated CO_2. Values are means ± 1 SE, $N = 64$ plots.

change manipulation of a complete ecosystem with thousands of plants and a full suite of plant, animal, microbial, and soil processes. The annual life cycle of the dominant plants allows relatively brief experiments to span several complete generations (*17*).

We investigated the impacts of individual and multiple simultaneous global changes on NPP of a moderately fertile California annual grassland (*18*), using the Jasper Ridge Global Change Experiment (JRGCE). The JRGCE involved four global change factors at two levels: CO_2 [ambient and 680 parts per million (ppm)], temperature (ambient and ambient plus 80 W m^{-2} of thermal radiation), precipitation (ambient and 50% above ambient plus 3-week growing season elongation), and N deposition (ambient and ambient plus 7 g of N m^{-2} $year^{-1}$) in a complete factorial design. The JRGCE, initiated in 1998, includes eight replicates of each of the 16 treatments. These are organized as a split-plot design with 32 circular plots, each divided into four 0.78-m^2 quadrants, separated by solid partitions below ground and mesh partitions above ground (Fig. 1) (*19*). Manipulations began at the start of the 1998–1999 growing season. Each year, we estimated NPP as peak biomass (above and below ground) in late spring (*20*).

Over the first 2 years of the manipulations and across all of the treatment combinations, elevated CO_2 had no significant effect on NPP (*21*) (Fig. 2). In the third year, 2001, the mean NPP for all treatment combinations with elevated CO_2 was 988 ± 52 g m^{-2} versus 1089 ± 54 g m^{-2} for all treatment combinations with ambient CO_2 ($P = 0.081$). The absence of significant biomass increases in response to elevated CO_2 is consistent with several prior studies at the ecosystem scale (*8*, *9*, *14*, *22–24*) but contrasts sharply with the results of most greenhouse experiments and many ecosystem studies, where elevated CO_2 leads to increased aboveground growth (*25–28*).

In the third year of manipulations of the JRGCE, elevated CO_2 stimulated aboveground biomass in the treatment in which all of the other factors were at ambient levels. Aboveground biomass in the ambient CO_2 treatment was 469 ± 27 g m^{-2}, and adding CO_2 increased this to 622 ± 24 g m^{-2} ($P = 0.003$, table S1) (*29*). This comparison parallels results of many other single-factor CO_2 experiments. The 32.6% increase in aboveground biomass is comparable to the 25% increase observed in North Carolina pine plantations (*25*) and the 20 to 43% increase in crop plants at the Arizona Free-Air CO_2 Enrichment (FACE) site (*15*, *26*).

Each of the treatments involving increased temperature, N deposition, or precipitation (alone or in combination) tended to increase aboveground biomass and NPP, but elevated CO_2 consistently dampened these increases (Fig. 3) (*29*). The three-factor combination of increased temperature, precipitation, and N deposition produced the largest stimulation of NPP (84%, $P = 0.021$), but the addition of CO_2 reduced this to 40% ($P = 0.028$). The suppressive effect of elevated CO_2 was even clearer for below ground biomass, where the average effect across all treatments was a decrease of 22% ($P = 0.005$) (*21*).

The NPP response of this ecosystem to multiple global changes was not a simple combination of responses to individual global change factors. Some treatment combinations (such as warming and precipitation) led to intermediate responses, with NPP near the average of the single-factor responses (Fig. 3). Others (such as warming and N deposi-

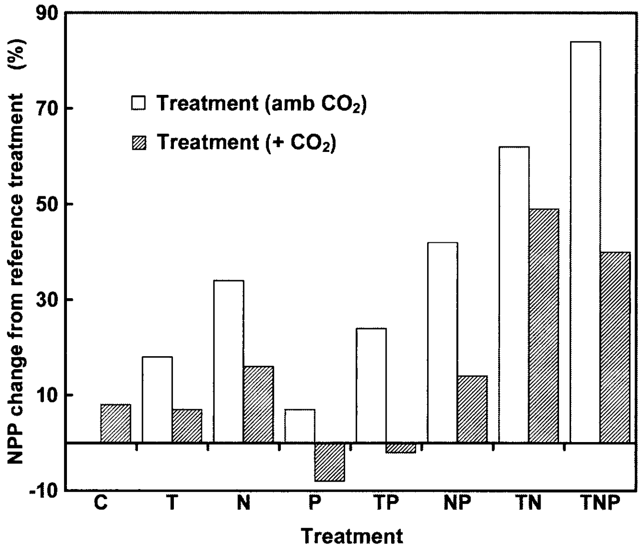

Fig. 3. Percent changes in NPP for each treatment, relative to corresponding reference. For each treatment combination, the reference is defined as all ambient CO_2 plots in which the variable(s) that defines each treatment combination are also at ambient. amb, ambient; C, elevated CO_2; N, N deposition; T, increased temperature; P, increased precipitation. For treatments T, N, and P, $n = 24$ plots. For treatments TP, NP, and TN, $n = 12$. For treatments C and TNP, $n = 6$. For example, the open bar for the increased temperature pair (T) is calculated using all treatments with increased temperature but not elevated CO_2 ($n = 24$). The gray bar in the same pair is calculated using all treatments with increased temperature and elevated CO_2 ($n = 24$).

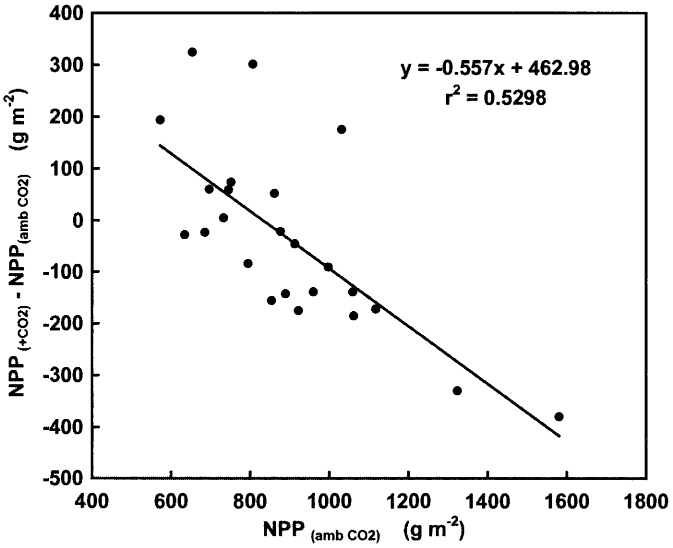

Fig. 4. The effect of elevated CO_2 on NPP in relation to NPP under ambient CO_2 for the eight treatment pairs with and without elevated CO_2 (*30*) for each of the 3 years of treatment. Each point is the mean for all replicates ($n = 8$) in one treatment pair in 1 year.

tion) were approximately additive (Fig. 3). Across the seven treatment combinations involving elevated CO_2 and at least one other factor (*30*), the addition of elevated CO_2 decreased NPP ($P = 0.048$) (*31*), which is the opposite of the effect of CO_2 as a single factor (Fig. 3).

Thousands of published papers describe plant or ecosystem responses to elevated CO_2 (*32*). Generally, stimulatory responses in individual plants (*27*) often persist at the ecosystem scale, in the form of increased aboveground growth. Relatively few studies address ecosystem NPP responses (above- and belowground). Those that do include examples of substantial NPP increases as well as modest responses and no change (*33*). Only a few studies address the effects of elevated CO_2 in combination with other global changes at the ecosystem scale. Oechel *et al.* (*9*) found that warming could extend the time over which elevated CO_2 stimulated NPP in arctic tundra. Oren and colleagues (*8*) observed a parallel result with N addition in a pine plantation. Reich *et al.* (*6*) reported increased sensitivity of NPP to elevated CO_2 with added N, but only when species diversity was high. Several studies from agricultural ecosystems also demonstrate that enhanced N availability can lead to larger increases in NPP in response to elevated CO_2 (*34*). In all these studies on N-limited ecosystems, the sensitivity of NPP to elevated CO_2 increased with the addition of N or, in the tundra example, with a treatment that indirectly increased N availability.

The JRGCE results suggest a fundamentally different kind of ecosystem response. Previous studies indicate that enhanced availability of a limiting resource such as N increases an ecosystem's potential to take advantage of elevated CO_2. Our results are more consistent with the idea that, under some circumstances, elevated CO_2 can constrain potential NPP. Several aspects of the JRGCE might account for this contrast. To our knowledge, this is the only ecosystem-scale experiment to date in which the treatments have been applied through several generations of the dominant plants. It is one of very few experiments to explore interactions between warming and elevated CO_2 at the ecosystem scale. It is also one of few ecosystem experiments to simulate N deposition with nitrate (the primary form delivered from the atmosphere in most locations) as opposed to a mixture of nitrate and ammonium.

Several mechanisms could contribute to the suppressive effects of elevated CO_2 reported here. First, it is possible that the responses depend on specific features of the treatments. Simulating N deposition with nitrate may shift the plants from ammonium to nitrate nutrition, which may make them less sensitive to elevated CO_2 than those grown on ammonium (*35*). The response of grassland NPP to elevated CO_2 is often greatest when water is limiting (*36*). CO_2-driven alleviation of water stress through decreases in transpiration may nullify any stimulatory effect of added precipitation. Although both of these mechanisms potentially account for a decrease in CO_2 sensitivity, neither is likely to result in a suppressive effect of elevated CO_2.

Second, it is possible that the suppressive effect of CO_2 is a consequence of changes in plant species richness or other aspects of plant community composition. The structure of the plant community was dynamic in the JRGCE. However, the changes in plant species richness and abundance were similar in the single- and multifactor CO_2 treatments (*37*), arguing against a major role for community composition in explaining the suppressive effect of elevated CO_2 on NPP in multifactor treatments only.

A third possibility is that the suppressive effect of elevated CO_2 is a consequence of limitation by some soil nutrient. This could result from gradual immobilization of a limiting nutrient by soil microorganisms under elevated CO_2, reflecting increased demand by microbes more richly supplied with carbon lost from roots (*38*–*40*). Several indicators of soil metabolic activity were enhanced under elevated CO_2 (*41*, *42*). Nutrient limitation under elevated CO_2 could also be a consequence of decreased root allocation, which tends to limit the capacity of plants to forage for nutrients. The effects of decreased root allocation should be most severe in settings where NPP is high, because NPP drives plant resource demand. In most settings, plants respond to nutrient limitation with an increase in root allocation (*43*). In the results presented here, however, root allocation consistently decreased in response to elevated CO_2, a pattern that may or may not effectively balance nutrient supply and demand (*44*).

Previous studies at Jasper Ridge grasslands (*45*) and many other ecosystems documenting the potential for limitation by phosphorus make it an interesting candidate as a limiting nutrient. It is also possible that N becomes limiting when NPP is increased and CO_2 is elevated. N limitation in the treatments with N deposition, however, would require that the additional N be only sparingly available, as a result of either its form or the timing of its application.

Some of the strongest evidence for the nutrient limitation mechanism comes from the multiyear response. Over all 3 years of manipulations in the JRGCE and all treatment combinations, elevated CO_2 tended to be stimulatory when NPP was low and suppressive when NPP was high (Fig. 4). In the eight pairs of treatment combinations with ambient and elevated CO_2, NPP under ambient CO_2 explained 53% of the effect of adding CO_2, with consistent suppressive effects at levels of NPP greater than 800 g m^{-2}. This result, closely paralleling that for several ecosystems studied with single-factor manipulations (*24*), provides further support for the hypothesis that negative effects of elevated CO_2 reflect constraints from a resource that becomes increasingly limiting as demand for it increases.

We do not yet know the contribution of each of these mechanisms to the overall response, but probably all contribute. Experiments to test the involvement of each are now underway.

This report of suppressive effects of elevated CO_2 has a strong message for global change research. Ecosystem responses to realistic combinations of global changes are not necessarily simple combinations of the responses to the individual factors. Accurate predictions of ecosystem responses to suites of global changes depend on successful integration across a range of processes and time scales. Multifactor experiments on ecosystems that are easy to manipulate can provide a rich source of examples as well as test beds for exploring hypotheses with the potential to explain the responses of a wide range of ecosystems. Future experiments should develop theoretical and empirical frameworks for integrating information from these model ecosystems with information from less-easily studied ecosystems that play important roles in the carbon cycle.

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18. Research was conducted at Stanford University's Jasper Ridge Biological Preserve in central California (37°24'N, 122°14'W, elevation 150 m) between October 1998 and June 2001. The grassland is dominated by annual grasses (*Avena barbata* and *Bromus hordeaceus*) and forbs (*Geranium dissectum* and *Erodium botrys*). Typical of a Mediterranean climate, the growing season (October to May) is cool and wet, and the summer (June through September) is hot and dry.
19. Control, warming, elevated CO_2, and warming plus elevated CO_2 treatments were each applied to eight plots. Infrared heat lamps were suspended over the centers of the warming plots, heating the plant canopy by 0.8° to 1°C. Atmospheric CO_2 concentrations were elevated to ~680 ppm with a ring of free-air emitters surrounding each plot and delivering pure CO_2 at the canopy level. Control, N deposition, increased precipitation, and N plus increased precipitation treatments were randomly assigned to the four quadrants in every plot. We applied N as $Ca(NO_3)_2$ at the rate of 7 g of N m^{-2} $year^{-1}$, with an initial application of 2 g of N m^{-2} at the first rains and a second application of 5 g of N m^{-2} applied as slow-release fertilizer in the first week of January each year. We augmented ambient precipitation events by 50% with drip irrigation and overhead sprinklers and added an additional two rain events in the spring to extend the rainy season by approximately 3 weeks. After 1 year of preliminary measurements, we began treatments in November 1998. Each of the 16 possible combinations of CO_2, temperature, N deposition, and precipitation was replicated 8 times.
20. We measured aboveground biomass on two dates, 1 month apart, by harvesting all live and senesced vegetation and litter within a designated harvest area. We report the greater of the two harvests for each treatment. Three 22-mm-diameter soil cores made to a depth of 15 cm were taken within the aboveground harvest area, 2 days after the first aboveground harvest. Soils were wet-sieved through 0.5-mm mesh. Live roots were separated from dead roots. We did not account for additional NPP in root turnover, which, on the basis of other studies at this site, may increase annual root production by 44 to 54% (*46*).
21. We analyzed NPP, aboveground biomass, and belowground biomass using a split-plot analysis of variance with two levels each of CO_2, warming, precipitation, and temperature. The full model is described in (*37*). The data were logarithmically transformed.
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29. A Student's *t* test paired by block was performed on logarithmically transformed data. See supporting online material available on *Science* Online.
30. The 16 experimental conditions can be viewed as 8 pairs in which the members of a pair are identical except that one set of replicates experiences ambient CO_2 and one set experiences elevated CO_2. Seven of these eight pairs have elevated levels of one or more of the following factors: warming, precipitation, or N inputs (see supporting online material).
31. A Student's *t* test paired by block was performed to determine the effect of elevated CO_2 on NPP under all treatment combinations, except control and elevated CO_2 alone. This was a posthoc test of the hypothesis that, in the presence of at least one other global change factor, the effect of elevated CO_2 was to decrease NPP. The data were logarithmically transformed.
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Supporting Online Material

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Table S1

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