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Interactive Effects of Fire, Elevated Carbon Dioxide, Nitrogen Deposition, and precipitation on a California Annual Grassland

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ABSTRACT

Although it is widely accepted that elevated atmospheric carbon dioxide (CO_2), nitrogen (N) deposition, and climate change will alter ecosystem productivity and function in the coming decades, the combined effects of these environmental changes may be nonadditive, and their interactions may be altered by disturbances, such as fire. We examined the influence of a summer wildfire on the interactive effects of elevated CO_2, N deposition, and increased precipitation in a full-factorial experiment conducted in a California annual grassland. In unburned plots, primary production was suppressed under elevated CO_2. Burning alone did not significantly affect production, but it increased total production in combination with nitrate additions and removed the suppressive effect of elevated CO_2. Increased production in response to nitrate in burned plots occurred as a result of the enhanced aboveground production of annual grasses and forbs, whereas the removal of the suppressive effect of elevated CO_2 occurred as a result of increased aboveground forb production in burned, CO_2-treated plots and decreased root production in burned plots under ambient CO_2.The tissue nitrogen–phosphorus ratio, which was assessed for annual grass shoots, decreased with burning and increased with nitrate addition. Burning removed surface litter from plots, resulting in an increase in maximum daily soil temperatures and a decrease in soil moisture both early and late in the growing season. Measures of vegetation greenness, based on canopy spectral reflectance, showed that plants in burned plots grew rapidly early in the season but senesced early. Overall, these results indicate that fire can alter the effects of elevated CO_2 and N addition on productivity in the short term, possibly by promoting increased phosphorus availability.

Key words: carbon dioxide; climate change; disturbance; fire; global change; nitrogen; grassland; California.

INTRODUCTION

Human activities impact ecosystems by affecting both resource availability and disturbance. Elevated carbon dioxide (CO_2), nitrogen (N) deposition, and climate change are environmental factors that can each cause dramatic changes in primary

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production and plant species composition (Marrs and others 1983; Strain and Bazzaz 1983). However, these factors can have nonadditive effects in natural communities (Shaw and others 2002; Zavaleta and others 2003), and our ability to predict ecosystem responses to their simultaneous effects depends on our understanding of the mechanisms underlying their interactions.

Although some insights have been gained from recent studies on the interactive effects of environmental changes on plant communities, these interactions have not been examined in the context of disturbance. Fire is a disturbance that plays an important role in structuring many plant communities and altering ecosystem function, particularly in grasslands (Abrams and others 1986; Briggs and Knapp 1995; Noy-Meir 1995). The warmer and windier conditions that climate scenarios predict for some regions in the future, along with increased fuel loads, could increase the intensity and spread of fires (Fried and others 2004). There are numerous mechanisms whereby fire could alter the effects of environmental changes on ecosystems. For example, many responses to environmental change are species-specific, and fire can alter plant species composition directly by differentially damaging shoots and seeds (Pollack and Kan 1998). Soil Carbon (C) and N concentrations, aggregate formation, and soil microorganisms may also be altered by fire (Garcia-Oliva and others 1998; Fynn and others 2003; Andersson and others 2004). Alternatively, the effects of fire on production and species composition may be driven indirectly by the removal of surface litter. Litter removal eliminates a physical barrier to seedling emergence and fosters greater light transmission to the soil surface (Briggs and Knapp 1995; Heisler and others 2004). This greater insolation typically results in an increase in soil surface temperatures and a decrease in soil moisture (Hulbert 1969; Li and Herbert 2004). Along with nutrient deposition from ash, these changes in soil microclimate can alter microbial activity and nutrient availability (Turner and others 1997; Romanyà and others 2001).

We examined the effects of a summer wildfire on the interactive effects of environmental changes in the context of the Jasper Ridge Global Change Experiment (JRGCE), a full-factorial experiment initiated in 1998 to study the effects of elevated CO_2, N deposition, and climate change on an annual grassland community. Given the occurrence of the fire at a time when most annual plants had died, and the importance of nutrient cycling and litter dynamics as mechanisms driving the interactive effects of environmental factors in this system (Hungate and others 1997; Henry and others 2005), we anticipated that the largest effects of the fire would be indirect. We predicted that increased soil temperatures resulting from the removal of surface litter would result in more rapid early-season growth and increased total production, particularly in combination with water and CO_2 treatments, which would offset decreases in soil moisture in burned plots. Fire was also expected to alter the system's nutrient dynamics. It has been suggested that phosphorus (P) availability influences responses to global change treatments in this experiment (Cleland 2005). Earlier work has demonstrated that elevated CO_2 has a suppressive effect on other global change treatments at Jasper Ridge and that it decreases root allocation (Shaw and others 2002). We hypothesized that fire would promote greater productivity in CO_2-treated plots, particularly in combination with added nitrate, by alleviating P limitation, and that this would result in a decreased N:P ratio in plant tissue. Increased production was predicted to be highest in annual grasses, which have responded vigorously to nutrient additions in this system in the past (Zavaleta and others 2003).

METHODS

Site Description

The JRGCE is situated in the Jasper Ridge Biological Preserve, located in the eastern foothills of the Santa Cruz Mountains in central California, USA (37°40′ N, 122°22′ W, 120 m elevation). The region experiences a mediterranean-type climate, with a cool, wet growing season from November to May and a hot, dry summer. Cumulative precipitation from 1 October 2003 to 30 September 2004 was 546 mm; mean daily maximum temperature from 1 October 2003 to 31 May 2004 was 19.5°C. The corresponding cumulative precipitation and mean daily maximum temperature values from 1986 to 2003 averaged 677 mm and 19.3°C, respectively. The soils are fine, mixed, thermic Typic Haploxeralfs. They consist of weathered alluvium from the Franciscan complex, very deep and well drained (125–150 cm), and are classified as alfisols (Kashiwagi 1985). The annual nonnative grasses *Avena barbata* and *A. fatua* and, to a lesser extent, *Bromus hordeaceus* and *Lolium multiflorum* dominate the site. Nonnative forbs (for example, *Geranium dissectum*, *Erodium botrys*, and *Crepis vesicaria*) and native annual forbs (for example, *Hemizonia congesta* ssp. *luzulifolia* and *Epilobium brachycarpum*) also are present. Perennials constitute less than 10% of total biomass in 85% of the quadrants, with native grasses (for example, *Danthonia californica* and *Nassella pulchra*) often the dominant perennials.

Experimental Design

The experiment, initiated in 1998, includes four global change treatments (CO_2, warming, N, and water), each at two levels (ambient and elevated), in a full-factorial design. Treatments were organized in a randomized block split-plot design, with CO_2 and warming administered factorially at the plot level and N and water additions assigned factorially to the four quadrants in each plot (circular plots, 3.14 m^2 area; $n = 8$ for each treatment combination). On 26 July 2003, two of eight blocks experienced a wildfire. It was a rapid, low-intensity fire that ashed almost all aboveground litter in the burned plots. To increase the number of replicates (n) for each treatment combination in burned plots, warming, the treatment with the weakest effects over the first 5 years of the experiment, was not administered in these plots over the following growing season, which provided $n = 4$ for burned plots and $n = 6$ for unburned plots. Carbon dioxide was elevated to approximately 680 ppm by a ring of free-air emitters surrounding each plot that deliver pure CO_2 at the canopy level (Miglietta and others. 2001a, 2001b). Nitrogen was applied as $Ca(NO_3)_2$ with an application of 2 g N m^{-2} at the first rains and 5 g of N m^{-2} as slow-release fertilizer each January. For water additions, ambient rain was augmented by 50% with drip irrigation (1998–2000) and overhead sprinklers (2001–04), and two rain events were simulated in the spring to extend the rainy season by approximately 3 weeks. Plots and quadrants were separated belowground by fiberglass panels to a depth of 0.5 m, and quadrants were separated aboveground by netting. The experiment was fenced to exclude herbivory by deer in the wet season, and gopher activity was minimized by both trapping and installing belowground barriers.

Biomass and Tissue Chemistry

Two aboveground biomass harvests (20 April and 10 May 2004) were conducted to account for differences among treatments in the timing of peak biomass, and the maximum value for each quadrant was used to estimate peak biomass. For each harvest, all aboveground plant matter in a 141-cm^2 area was collected. Plants were sorted to species level for the first harvest and to functional-group level (annual grasses, perennial grasses, annual forbs, perennial forbs, legumes, and woody plants) for the second harvest. Seasonal trends in vegetation greenness were quantified based on canopy spectral reflectance (normalized difference vegetation index, or NDVI), measured under cloud-free conditions using a portable spectroradiometer (Analytical Spectral Devices, Boulder, CO, USA) that was normalized to a spectrally neutral reference panel (Spectralon; Labsphere, North Sutton, NH, USA,). Root biomass was determined by separating live roots from two 30-cm–deep soil cores collected during the first biomass harvest. All biomass was oven-dried at 60°C for a minimum of 4 days before weighing. For annual grasses, total N and P were measured as PO_4 and NH_4 on an AP300 auto analyzer (Astoria Pacific, Clackamas, OR, USA) after Kjeldahl digestion.

Soil Microclimate Measures

Soil moisture was measured by time domain reflectometry, using rods that extended from the surface to depths of 15, 30, and 45 cm at approximately the same locations in each quadrant. Data were gathered every 2–4 weeks. Soil temperature data were obtained at hourly intervals from thermocouples buried at 2 and 10 cm below the soil surface in each quadrant.

Data Analyses

Dependent variables were analyzed using a split-plot analysis of variance (ANOVA) that included CO_2 and burning as fixed between-plot factors, water and nitrate as fixed within-plot factors, and interaction terms for all treatment combinations (warmed, unburned plots were excluded from all analyses because of the absence of warmed, burned plots). Error terms for significance tests were as specified in Kirk (1995). The analysis was run using the REML method of the Fit Model platform in JMP 4.0 (SAS Institute, Cary, NC, USA). Aboveground and belowground plant biomass were used to estimate aboveground and belowground net primary production (ANPP and BNPP), respectively. Aboveground biomass is a reasonable approximation for ANPP given that the majority of biomass in this system is produced by annual plants. The use of belowground plant biomass to estimate BNPP does not account for root turnover losses. Minirhizotron data from this grassland indicate that cumulative root production over the growing season is 54% higher than peak standing root biomass, and rates of root turnover do not differ between CO_2-treated and ambient plots (Higgins and others 2002). Estimates of BNPP, both corrected for root turnover and not corrected, are presented here.

Daily soil temperature data were averaged over two distinct intervals for ANOVA: from mid-December through the end of February, when maximum daily soil temperature in control plots remained stable below 15°C, and from March through the end of April, when maximum daily soil temperatures rose above 15°C. Soil moisture data were also averaged over two intervals: early season (November) and late season (March through mid-May). Both intervals corresponded with periods when soil moisture in control plots was below 25%. Vegetation greenness data were averaged from December through the end March. The timing of peak vegetation greenness and half of peak greenness were also analyzed. Data were log- or square root–transformed to improve normality when necessary.

RESULTS

In unburned plots, elevated CO_2 suppressed total production (Figure 1, CO_2 × burn, $P = 0.028$) by suppressing the growth of roots (pooled over all species) and forb shoots (Figure 2ii and iv; full ANOVA results displayed in Table 1). Although burning alone had no significant effect on production, total production increased significantly in nitrate-treated plots in combination with burning (Figure 1, burn × N, $P = 0.01$) as a result of the increased aboveground production of annual grasses and forbs (Figure 2i, ii). The suppressive effect of elevated CO_2 on total production was removed by burning (Figure 1, CO_2 × burn, $P = 0.028$) as a result of increased aboveground forb production in burned, CO_2-treated plots and decreased root biomass in burned plots under ambient CO_2 (Figure 2ii, iv). Increases in production did not coincide with changes in species richness (Table 1), and one species (*Erodium botrys*) was primarily responsible for increases in aboveground forb production in response to burning, CO_2, and nitrate. An apparent decrease in the category "other shoots" (the sum of perennial grasses, perennial forbs, and legumes) in burned plots (Figure 2iii) was explained by the existence of a patch of perennial grasses in an unburned corner of the experiment prior to the fire. Root production did not increase in response to the combination of burning and nitrate (Figure 2iv), and the ratio of belowground (root) to aboveground production decreased in response to both burning ($P = 0.04$) and elevated CO_2 ($P = 0.04$) (Tables 1 and 2). The N:P ratio in the aboveground tissue of annual grasses increased with nitrate addition ($P < 0.001$) and decreased with burning ($P = 0.04$) (Tables 1 and 2).

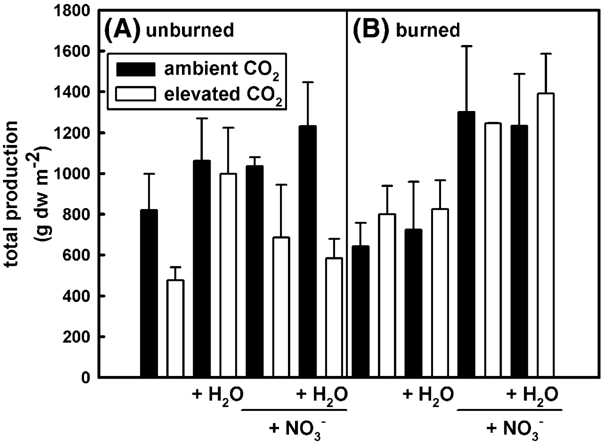

Figure 1. Total net primary production in **a** unburned plots and **b** burned plots of the Jasper Ridge Global Change Experiment, as estimated from aboveground and belowground plant biomass. Two aboveground biomass harvests (20 April and 10 May 2004) were conducted to account for differences among treatments in the timing of peak biomass, and the maximum value for each quadrant was used to estimate peak biomass. Error bars denote SE ($n = 6$ for unburned plots and $n = 4$ for burned plots). Significant treatment effects ($P < 0.05$) from four-way split-plot ANOVA: NO_3, $P = 0.003$; NO_3 × burn, $P = 0.01$; CO_2 × burn, $P = 0.028$.

In control plots, maximum daily soil temperature at 2-cm depth remained below 15°C until March, then rose to over 25°C by mid-April (Figure 3a). Maximum soil temperatures were elevated by 1°–12°C in burned plots, with the highest increases occurring early in the season before plant cover was well established (Figure 3b, $P < 0.001$; full ANOVA results shown in Table 3). Maximum soil temperatures in nitrate-treated plots decreased relative to untreated plots when plant biomass increased (Figure 3b, $P = 0.001$). Soil moisture at 0–30-cm depth in control plots rose above 25% in early December, peaked at the end of February, and fell sharply to below 25% in early March (Figure 4a). Burned plots had lower soil moisture than unburned plots both early and late in the season when soil moisture was low (Figure 4b, $P = 0.008$ and $P = 0.02$, respectively), whereas both water and CO_2 treatments had high soil moisture relative to untreated plots ($P < 0.001$ and $P = 0.03$, respectively). Vegetation greenness increased rapidly in burned plots, but it declined earlier in these plots than in unburned plots at the end of the season (Figure 5, $P = 0.01$ and $P < 0.001$, respectively).

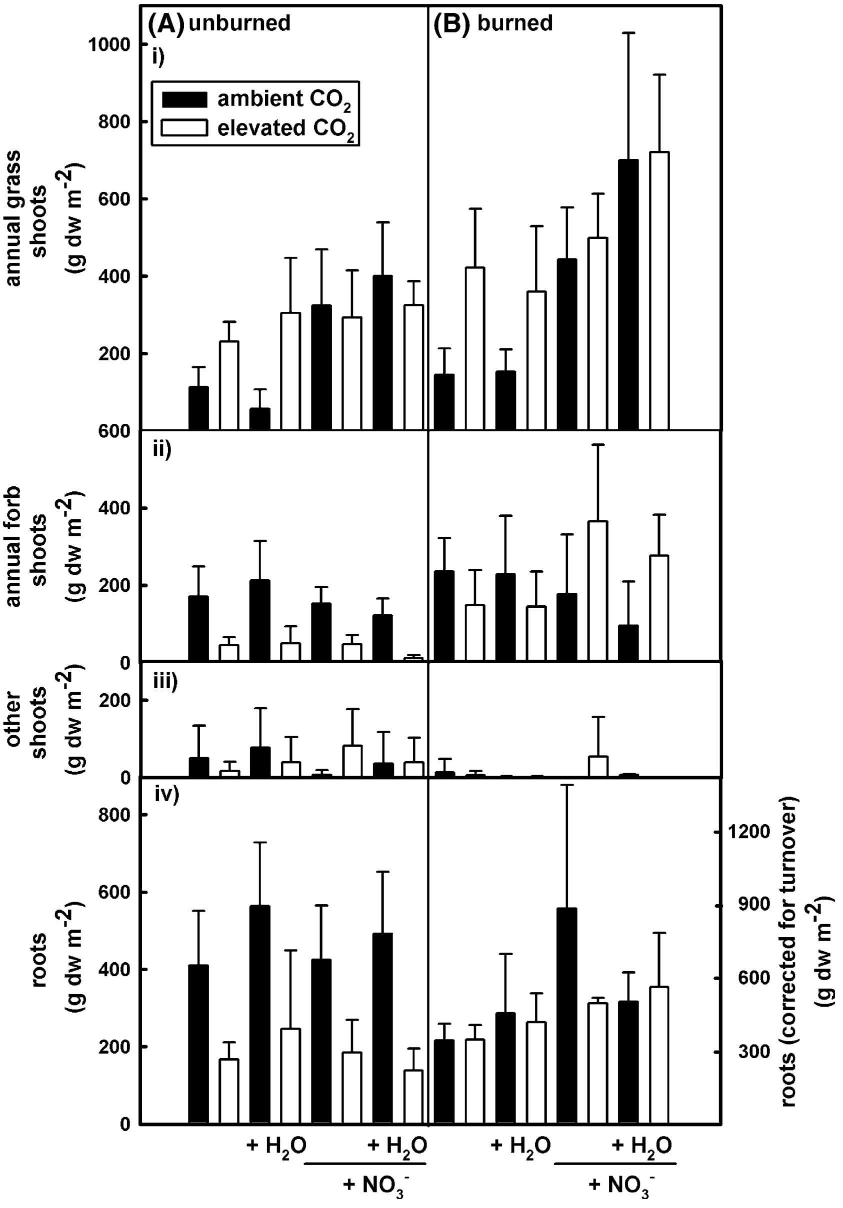

Figure 2. Contribution to net primary production in **a** unburned plots and **b** burned plots of *i* aboveground annual grasses, *ii* aboveground annual forbs, *iii* other shoots (including perennial grasses, perennial forbs, and legumes), and *iv* roots of all species, as estimated from peak biomass. Root production estimates, both corrected for turnover losses (right y-axis) and uncorrected (left y-axis), are presented. Error bars denote SE ($n = 6$ for unburned plots and $n = 4$ for burned plots). Significant treatment effects ($P < 0.05$) from four-way split-plot ANOVA: *i* NO_3, $P < 0.001$; $NO_3 \times CO_2$, $P = 0.006$; *ii* burn, $P = 0.045$; $NO_3 \times CO_2$, $P = 0.046$; *iv* CO_2, $P = 0.028$.

DISCUSSION

Our results demonstrate that fire can alter the effects of environmental changes on productivity, even when productivity is not affected by fire alone. Although periodic burning (less than 1 y^{-1}) at light to moderate intensities often increases productivity in tallgrass prairie (Abrams and others 1986; Briggs and Knapp 1995), such increases are typically not observed in shortgrass prairie or where litter accumulation is low (Launchbaugh 1964; Hulbert 1969). In the JRGCE, burning alone did not increase overall production; however, it increased production in combination with nitrate additions and removed the suppressive effect of elevated CO_2 on production. Although burning did not alter the interactive effects of CO_2 and nitrate additions significantly, unlike in previous years (see, for example, Shaw and other 2002), there was no significant interaction between CO_2 and nitrate in unburned plots.

Increases in production after burning have been hypothesized to result from the effects of soil warming on microbial activity and nutrient mineralization, increased light penetration to the soil surface, or the deposition of limiting mineral nutrients from ash (Blair 1997; Li and Herbert 2004). Previously, Shaw and others (2002) and Cleland (2005) hypothesized that limitation by a mineral nutrient, potentially P, could explain the

Table 1. Summary of *P* Values from Four-way Split-Plot Analyses of Variance Testing for the Effects of Treatments on Estimates of Total, Aboveground, and Belowground Plant Production; Annual Grass Aboveground Nitrogen–Phosphorus Ratio; and Species Richness

		Aboveground Production		Belowground production			
Effect	Total Production	Annual Grasses	Annual Forbs	All Species	Below:Above	N:P	Species Richness
C	0.164	0.147	0.262	0.028[a]	0.039[a]	0.947	0.126
B	0.145	0.067	0.045[a]	0.844	0.040[a]	0.042[a]	0.421
W	0.165	0.287	0.272	0.676	0.742	0.169	0.112
N	0.003[b]	<0.001[c]	0.701	0.382	0.153	<0.001[c]	0.748
C × B	0.028[a]	0.785	0.078	0.082	0.923	0.248	0.347
W × N	0.131	0.144	0.159	0.082	0.128	0.240	0.447
C × N	0.248	0.006[b]	0.046[a]	0.596	0.710	0.484	0.456
B × N	0.010[a]	0.297	0.206	0.103	0.600	0.497	0.522
C × W	0.794	0.881	0.792	0.889	0.597	0.144	0.339
B × W	0.341	0.516	0.684	0.672	0.766	0.944	0.091
C × B × N	0.675	0.694	0.065	0.995	0.964	0.764	0.146
C × B × W	0.920	0.485	0.598	0.455	0.471	0.812	0.69
C × W × N	0.411	0.587	0.996	0.773	0.474	0.426	0.878
B × W × N	0.211	0.452	0.902	0.902	0.289	0.159	0.542
C × B × W × N	0.139	0.456	0.816	0.213	0.974	0.697	0.542

Treatments: N, nitrate; C, carbon dioxide; W, water; B, burned.

[a] *Significant at 0.05–0.01.*

[b] *Significant at 0.01–0.001.*

[c] *Significant at <0.001.*

Table 2. Means and SE from Significant Treatment Effects on Belowground:Aboveground Production (All Species) and Shoot Nitrogen:Phosphorus Ratio, % Nitrogen and % Phosphorus (Annual Grasses)

	Belowground: Aboveground			Nitrogen: Phosphorus		% Nitrogen		% Phosphorus	
Treatment	Mean	S.E.	Treatment	Mean	S.E.	Mean	S.E.	Mean	S.E.
Ambient	1.33	0.26	Ambient	6.5	0.4	1.14	0.09	0.142	0.013
B	0.81	0.21	B	5.1	0.2	0.96	0.03	0.146	0.006
CO_2	0.80	0.11	N	13.8	1.0	1.87	0.15	0.110	0.008
B and CO_2	0.46	0.08	B and N	11.7	0.8	1.26	0.06	0.086	0.004

Treatments: N, nitrate; CO_2, carbon dioxide; B, burned.

suppressive effect of elevated CO_2 on other treatment effects in this experiment. Although we could not separate the effects of microclimate and ash deposition, it appears, based on decreases in the N:P ratio of annual grasses from burned plots, that the alleviation of P limitation could have contributed to interactions between fire and the experimental treatments in the JRGCE. The stimulation of production by elevated CO_2 alone, observed in previous years of this experiment (see, for example, Shaw and others 2002), is consistent with this hypothesis; however, this would imply that P limitation occurred in those years at levels of production modestly higher than those present in control plots. Plants in CO_2-treated plots may be susceptible to P limitation at increased levels of productivity as a result of decreased root allocation. Conversely, decreased root allocation would not impede productivity in the burned plots because of increased P availability. Increased productivity after fire has been attributed in some systems to increased N mineralization, which typically occurs in systems where fire frequency is low to moderate (Risser and Parton 1982; Hulbert 1988; Romanyà and others

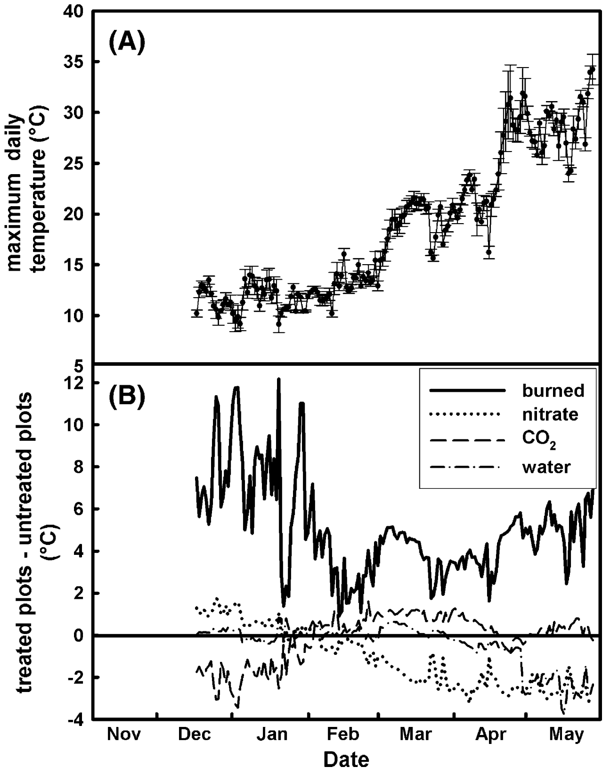

Figure 3. **a** Maximum daily soil temperature at 2 cm below the surface in control plots of the Jasper Ridge Global Change Experiment in 2003–04. Error bars denote SE (*n* = 6). **b** Differences in maximum daily soil temperature at 2 cm between treated and untreated plots, pooled over all other treatments.

2001). Although the stimulatory effect of nitrate on production indicates that our system is indeed N-limited, the lack of a stimulatory response to burning alone suggests that fire did not increase plant N availability meaningfully in the JRGCE.

Microclimatic changes resulting from litter removal may also stimulate plant growth after fire (Knapp and Seastedt 1986). We predicted that increased soil temperatures resulting from the removal of standing litter might increase production, particularly in combination with water and CO_2, both of which would offset decreases in soil moisture in burned plots. Although burned plots treated with water or elevated CO_2 were indeed warmer and wetter than control plots, water additions to burned plots did not stimulate productivity. Furthermore, although burned plots were relatively dry at the beginning of the season, they were no drier than control plots by the middle of the season, when soils were at field capacity. Decreases in soil moisture in burned plots relative to control plots later in the season may have resulted from the increased transpiration associated with increased plant biomass. As indicated by measures of canopy greenness, plants in burned plots began to senesce early, likely as a result of a decrease in soil moisture. The use of two biomass harvests helped to account for differences in peak biomass among treatments. In unburned plots, accumulated plant litter delayed early-season increases in canopy greenness, and canopy greenness was low in CO_2–treated plots. It should be noted that differences in canopy greenness among treatments may not be proportional to differences in biomass as a result of variation in accumulated litter and leaf turnover, and the saturation of greenness at high biomass.

Although the effects of fire on species composition are variable depending on the timing and intensity of burning (Parsons and Stohlgren 1989), fire often stimulates graminoid productivity preferentially over woody species and forbs (Abrams and others 1986). Notably, in California annual grasslands, fire has increasingly been used as a management tool to select native species over exotics and perennials over annuals (Dyer 2002, 2003; Gillespie and Allen 2004). Over the short term in the JRGCE, both grass and forb production were stimulated by the interactive effects of fire and CO_2 or nitrate, and annual species remained abundant. Species richness also was comparable between burned and unburned plots. However, perennials are not abundant in the experimental plots, with the exception of an unburned corner of the experiment site that contains a high proportion of perennial grasses. Also, as is typical of annual grasslands, the fire occurred after most of the plants had set seed, which would reduce the direct effects of fire on species composition. Although fire may affect soil microbial communities directly, particularly fungi (Dunn and others 1985), significant destruction of soil microbes is unlikely in annual grassland fires, which are fast-moving and of low intensity. Nevertheless, changes in soil microclimate (Garcia-Oliva and others 1998; Dyer 2003; Michelsen and others 2004) or the deposition of macronutrients such as potassium, calcium and magnesium from ash (Li and Herbert 2004) may have affected microbial activity throughout the growing season.

The results of this experiment indicate that fire plays an important role in modifying the effects of multiple environmental changes on ecosystem productivity. They also support the hypothesis that P limitation explains the suppressive effect of elevated CO_2 on other global change treatments in this experiment. Nevertheless, not only is it important to establish how these short-term responses will extrapolate to the longer term, but the

Table 3. Summary of *P* Values from Split Plot Analyses of Variances Testing for the Effects of Treatments on Maximum Daily Soil Temperature at 2-cm Depth, Soil Moisture from-0 to 30-cm Depth, and Canopy Greenness Measures

	Maximum Soil Temperature		Soil Moisture			Canopy Greenness	
Effect	19 Dec–Feb	Mar–Apr	Nov	Mar–15 May	Dec–Mar	Timing of Peak/2	Timing of Peak
C	0.406	0.427	0.079	0.025^a	0.015^a	0.310	0.147
B	<0.001^c	<0.001^c	0.008^b	0.018^a	<0.001^c	0.014^a	<0.001^c
W	0.901	0.823	0.023^a	<0.001^c	0.859	0.092	0.530
N	0.884	0.001^b	0.983	0.011^a	0.639	0.359	0.945
C × B	0.764	0.040^a	0.900	0.840	0.023^a	0.502	0.037^a
W × N	0.554	0.641	1.000	0.044^a	0.539	0.316	0.648
C × N	0.150	0.435	0.129	0.598	0.639	0.803	0.652
B × N	0.212	0.616	0.973	0.442	0.004^b	0.486	0.934
C × W	0.688	0.749	0.243	0.924	0.084	0.182	0.155
B × W	0.487	0.553	0.974	0.954	0.294	0.537	0.654
C × B × N	0.373	0.737	0.785	0.869	0.392	0.403	0.764
C × B × W	0.711	0.678	0.135	0.726	0.638	0.835	0.365
C × W × N	0.880	0.657	0.011^a	0.034^a	0.435	0.729	0.148
B × W × N	0.624	0.040^a	0.832	0.585	0.567	0.488	0.522
C × B × W × N	0.870	0.919	0.842	0.497	0.944	0.847	0.855

Treatments: N, nitrate; C, carbon dioxide; W, water; B, burned.
Data averaged over months, as indicated.
''Timing of peak/2'' refers to the sampling date at which half of the value of peak canopy greenness was exceeded.
[a]*Significant at 0.05–0.01.*
[b]*Significant at 0.01–0.001.*
[c]*Significant at <0.001.*

effect of P addition in this system needs to be tested explicitly. Increases in production will increase the quantity of standing litter in subsequent growing seasons, and the shading effect of this litter may offset any increases in P availability. Furthermore, microbial P demand may increase in response to the high C:P ratio of litter, which could accentuate plant P limitation.

The results of this experiment also must be assessed in the context of the site's fire history. Based on surveys at Jasper Ridge and two similar sites, the mean fire return interval was 12.0 years also in San Mateo County and the median fire return interval was 10 years from 1615 to 1884, in the absence of fire suppression (Stephens and Fry 2005). However, over the last century, there has been a history of fire suppression at the JRGCE site. Therefore, although we observed that elevated CO$_2$ had a suppressive effect on other treatments prior to burning, this suppressive effect may not be representative of the responses of grasslands with a regime of more frequent fires.

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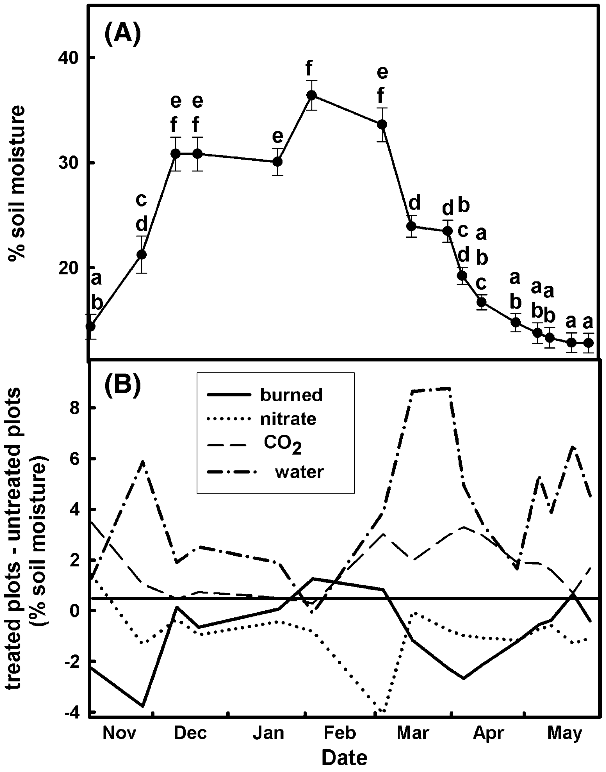

Figure 4. **a** Percent soil moisture integrated from 0 to 30 cm in control plots of the Jasper Ridge Global Change Experiment in 2003–04. Error bars denote SE (*n* = 6). A common letter above two means indicates that their differenceis not statistically significant (Tukey's Honestly Significant Difference test). **b** Differences in percent soil moisture integrated from 0 to 30 cm between treated and untreated plots, pooled over all other treatments.

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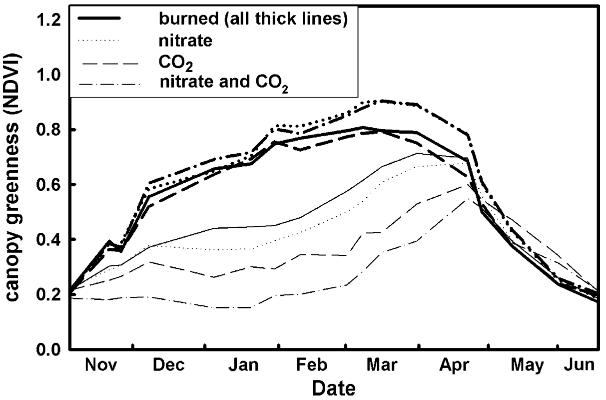

Figure 5. Seasonal trends in canopy greenness in plots of the Jasper Ridge Global Change Experiment in 2003–04 quantified based on canopy spectral reflectance (NDVI, normalized difference vegetation index). All thick lines denote burned treatments.

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