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Nitrogen limitation of microbial decomposition in a grassland under elevated CO_2

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Carbon accumulation in the terrestrial biosphere could partially offset the effects of anthropogenic CO_2 emissions on atmospheric CO_2 (refs 1, 2). The net impact of increased CO_2 on the carbon balance of terrestrial ecosystems is unclear, however, because elevated CO_2 effects on carbon input to soils and plant use of water and nutrients often have contrasting effects on microbial processes[3–5]. Here we show suppression of microbial decomposition in an annual grassland after continuous exposure to increased CO_2 for five growing seasons. The increased CO_2 enhanced plant nitrogen uptake, microbial biomass carbon, and available carbon for microbes. But it reduced available soil nitrogen, exacerbated nitrogen constraints on microbes, and reduced microbial respiration per unit biomass. These results indicate that increased CO_2 can alter the interaction between plants and microbes in favour of plant utilization of nitrogen, thereby slowing microbial decomposition and increasing ecosystem carbon accumulation.

Terrestrial ecosystems contain nearly three times more C (~2,060 Gt) than the atmosphere (~735 Gt C)[6] and may be either a significant C sink or source under future CO_2 models[7]. CO_2 enrichment often enhances ecosystem C gain in the short term through the stimulation of photosynthesis[2]. Over the long term, however, ecosystem C content depends on the balance between net primary production (NPP) and decomposition. Although increased CO_2 affects microbial processes by increasing C inputs to soil[3,4] and soil moisture[8,9], future ecosystem C content has been considered primarily in terms of nutrient supply to plants (C inputs) rather than CO_2 effects on decomposition (C loss). A large source of uncertainty is the effect of increased CO_2 on N availability to plants and microbes[10]. Because plants are commonly N-limited in terrestrial ecosystems[10,11], any tendency for increased CO_2 to decrease N availability can suppress the stimulation of NPP by elevated CO_2. Microbes can also be N limited[12,13], and a decrease in N availability due to increased CO_2 could decrease decomposition and enhance C storage. Conversely, N stimulation of C fixation under increased CO_2 may not necessarily translate into ecosystem C storage because increased N availability can also stimulate microbial decomposition and C turnover[14].

We used a sandstone grassland with moderate soil fertility to investigate the effect of increased CO_2 on microbial biomass and activity and on the interaction between plants and microbes in N acquisition. Experiments were conducted in an annual grassland at Stanford University's Jasper Ridge Biological Preserve in central California (37° 24′ N, 122° 14′ W; elevation 150 m) between 1992 and 1997. The climate is mediterranean with cool, wet winters and dry summers. Two CO_2 concentrations, ambient (360 p.p.m.) and increased (720 p.p.m.), were maintained for five years with open-top chambers (ten replicates for each treatment)[15,16]. Soil samples were collected on 26 November 1996, 23 March and 23 April 1997, corresponding approximately to early germination, peak physiological activity, and peak biomass of plants, respectively.

Annual NPP was either stimulated or not affected by increased CO_2 (refs 15, 16). By the end of the sixth growing season, plots exposed to increased CO_2 exhibited a moderate increase (2,750 g C m^{-2}) in the stock of below-ground organic C (soil, debris plus roots) compared with ambient controls (2,612 g C m^{-2}). Although this increase is not significant at $P = 0.05$, it is consistent with a moderate increase in C inputs[16]. We studied organic C

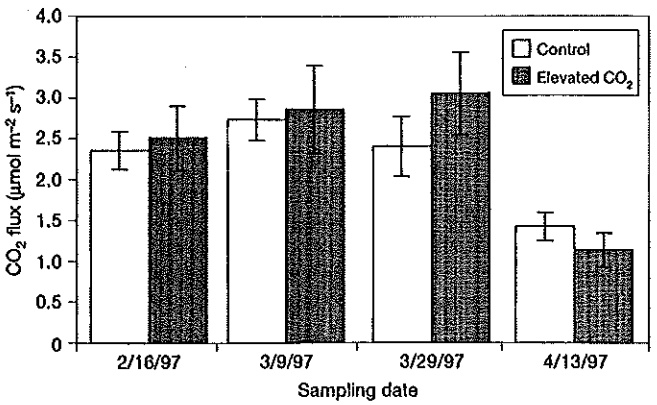

Figure 1 Below-ground respiration. Ambient (open bars) and elevated (filled bars) CO_2. Values are means ± standard error of the mean, s.e.m., $n = 5–6$ plots.

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turnover in the elevated CO_2 plots, based on the lower ^{13}C of the elevated CO_2. About 22% of total below-ground organic C originated from photosynthetic products during the 5.5-yr experiment. We also examined below-ground respiration (BR, the sum of root (RR) and heterotrophic microbial respiration (HR)) from mid-February to mid-April of 1997, the most active period of plant growth and decomposition. In contrast to the stimulation of BR by elevated CO_2 during the second year of the experiment (the 1993–94 growing season)[17], average BR was not significantly affected by CO_2 ($P = 0.514$; Fig. 1). This low response of BR to increased CO_2 occurred even though microbial biomass increased (see below). The C:N ratio of root biomass remained unchanged (data not shown), so respiration rate per unit root mass was probably unaffected by increased CO_2 (refs 18, 19). We conservatively estimated HR in the field by assuming that RR remained unchanged, although root biomass tended to be higher under elevated CO_2 (ref. 16). These estimates of HR per unit of microbial biomass decreased significantly under elevated CO_2 in the late growing season. However, concurrent laboratory incubation experiments indicated that C availability to soil microbes was significantly higher in soils under increased than under ambient CO_2. When soils sampled on 23 March were incubated at field moisture in the absence of plants, HR in elevated CO_2 plots ($64.81 \pm 2.90\ \mu g\ CO_2$ soil d^{-1}) was higher than in the ambient controls ($55.62 \pm 3.49\ \mu g\ CO_2\ g^{-1}$ soil d^{-1}) ($P = 0.058$), indicating that field HR was neither moisture- nor carbon-limited. Similarly, when soils sampled on 23 April were incubated at a constant moisture (20% w/w), HR in increased-CO_2 plots ($96.89 \pm 6.99\ \mu g\ CO_2\ g^{-1}$ soil d^{-1}) was higher than their ambient controls ($77.41 \pm 4.39\ \mu g\ CO_2\ g^{-1}$ soil d^{-1}) ($P = 0.015$). Together, these results suggest that microbial decomposition processes were suppressed in the middle to late growing season.

Increased CO_2 significantly decreased soil-extractable N late in the growing season (Fig. 2), when plant growth was most rapid. When plants were present (March and April), microbial biomass C was significantly higher in increased than in ambient CO_2 (Fig. 3a), but microbial biomass N remained unaffected by CO_2 increase (Fig. 3b), leading to higher C:N ratios in the microbial biomass (Fig. 3c). These results suggest that elevated CO_2 caused decreased N-availability to microbial biomass or an increased fungal/bacterial ratio. Early in the growing season before plants were major N consumers, microbial biomass C:N ratio was lower ($P = 0.068$), and there were more active bacteria (data not shown; $n = 5$; $P < 0.01$) in elevated than ambient CO_2. These data indicate that CO_2 enrichment increased N constraints on microbes at critical times during the year, with the net effect on microbes dependent on whether soil microbes were C- or N-limited.

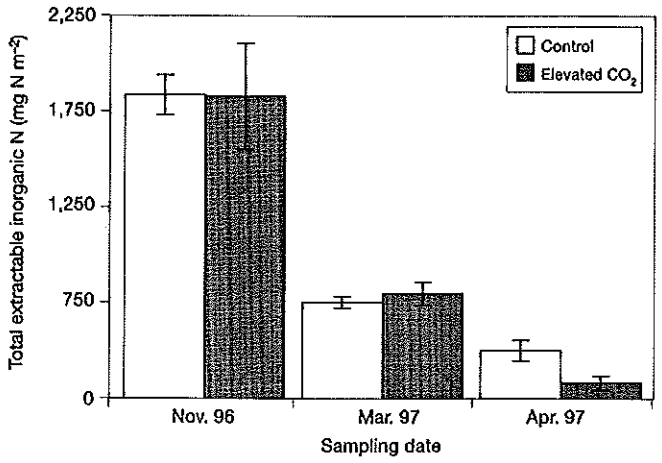

Figure 2 Extractable inorganic soil N over the growing season. Ambient (open bars) and elevated (filled bars) CO_2. Values are means ± s.e.m., $n = 10$ plots.

Studies addressing the effects of increased CO_2 on microbes have generally emphasized the importance of enhanced C-input for microbial biomass and activity[3,4,20], building on the assumption that microbes in soil are C-limited[21]. Little attention has been directed to the effects of increased CO_2 on plant and microbial use of N. We used ^{15}N as a tracer to investigate the impact of CO_2 enrichment directly on plant–microbial N partitioning during the middle to late growing season when N availability was low (Fig. 2). Results from the ^{15}N partitioning experiment indicate that increased CO_2 increased uptake of N by plants, leading to a substantial increase of ^{15}N in plant shoots and a corresponding decrease in the soil, but no change in the roots ($P = 0.867$) (Fig. 4a). ^{15}N in soil K_2SO_4 extracts and microbial biomass were 31% and 16% higher in ambient than elevated CO_2, respectively (Fig. 4b). These results show that increased CO_2 altered the interaction between plants and microbes in favour of plant N utilization. In response to N-limitation, plants may increase fine root production and/or mycorrhizal infection may increase[22]; both responses would serve to decrease the path length for diffusion of soil N in solution to roots.

Plant responses to increased CO_2 may affect soil microbial biomass and activity, either positively by increasing the availability of C and water, or negatively by reducing litter quality[23]. The effect of CO_2-driven N immobilization by plants on microbes has been largely overlooked. When N is available, increased C input caused by CO_2 enrichment stimulates microbial activity, especially N

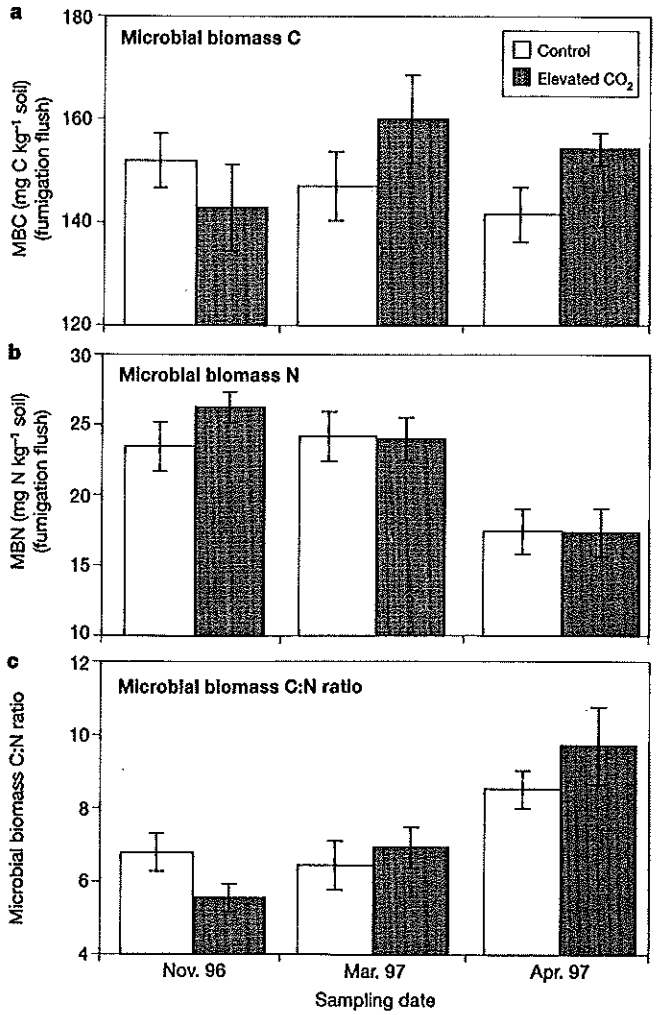

Figure 3 Microbial biomass carbon (a), nitrogen (b) and C:N ratios (c) in ambient (open bars) and elevated (filled bars) CO_2. Microbial biomass C and N (MBC and MBN) were the flush of organic C or N following the fumigation. Values are means ± s.e.m., $n = 10$ plots.

utilization[3,4,14]. Conversely, when N becomes limiting, competition between plants and microbes for N intensifies[13]. Enhanced C input and N limitation under increased CO_2 may favour fungi over bacteria[24] because fungal biomass has a lower C:N ratio and fungal hyphae can translocate nutrients. Root infection, hyphal length of arbuscular mycorrhizae, and concentration of glomalin, a glycoprotein produced by arbuscular mycorrhizal fungi, were higher in the elevated CO_2 plots than in the control in this grassland[25,26]. Enhanced production of fine roots and fungal hyphae could protect soil C by enhancing soil aggregation[27]. A soil community with greater fungal to bacterial biomass may be conducive to soil C retention[26,27]. Because the timing of active plant growth largely coincides with active decomposition[7], CO_2-induced decrease in available N for saprophytic microbes could lead to slower rates of decomposition. Increased plant N uptake under elevated CO_2 may, therefore, lay the foundation for a feedback loop in which the slow decomposition of residues retards the release of nitrogen[28], thereby constraining the plant response to increased CO_2.

Our results demonstrate that CO_2-enrichment in the atmosphere can exacerbate N constraints on microbes and suppress microbial use of soil C. Our findings also indicate that CO_2-driven changes in plant–microbe N partitioning could enhance C accumulation in terrestrial ecosystems under future CO_2 levels by increasing plant N-uptake, decreasing N availability for saprophytic microbes, and reducing rates of decomposition. This reduction in decomposition could cause terrestrial ecosystems to become net C sinks, especially if plants become more efficient at acquiring N from low C:N soil organic matter (for example, by increasing mycorrhizae[24]). Alternatively, if reduced rates of decomposition and resulting soil C accumulation decrease N supply to plants, this could decrease NPP and C inputs to soil, constraining the magnitude of C accumulation. Depending on the dynamics of N availability and species characteristics, a single ecosystem could experience N limitation predominantly through effects on the microbes at some times and effects on the plants at others. □

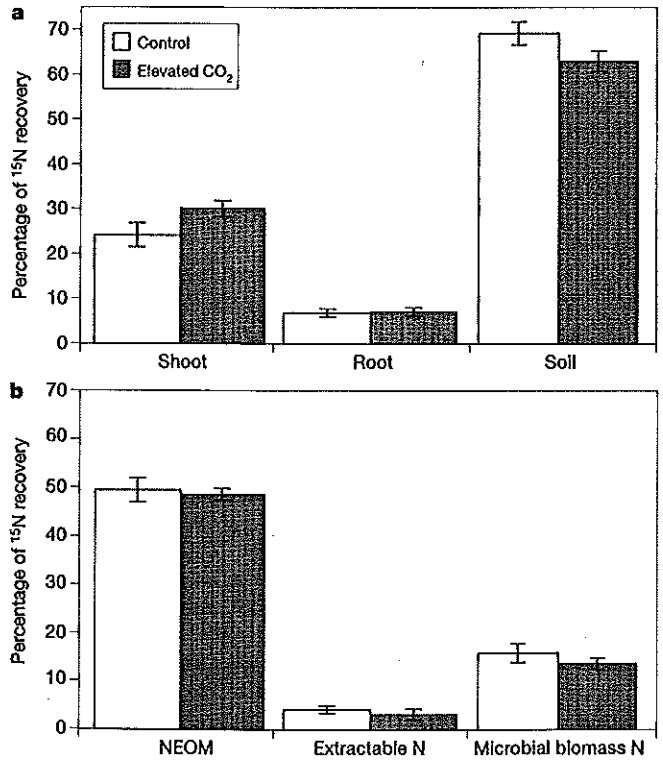

Figure 4 ^{15}N distribution, **a**, in plant shoots, roots, and soil and **b**, in non-extractable soil organic matter (NEOM), K_2SO_4 extracts and microbial biomass. Ambient (open bars) and elevated (filled bars) CO_2. Values are means ± s.e.m., $n = 10$ plots. Total microbial biomass ^{15}N in soil was calculated from microbial biomass ^{15}N flush by using an extraction efficiency of 0.45.

Methods

Field treatments and soil sampling

CO_2 fumigation began in January 1992 and has since been continuous except during the summer of 1992 following plant senescence. Open-top chambers were used to maintain the CO_2 concentration at ambient and approximately 720 p.p.m.[15]. Two 3.2-cm diameter soil cores were sampled to 15 cm depth from each plot on 26 November 1996 and 23 March 1997, and one 7.2-cm diameter core (15 cm depth) from each plot on 23 April 1997. Soil samples were sieved (2 mm), and roots and debris on the sieve were manually sorted and oven-dried. Soil, shoot, detrital and root carbon and nitrogen, and their isotope ratios were determined by combustion on a gas chromatography-mass spectrometer (GC-MS) (Europa Scientific Ltd.) using finely ground subsamples. We define below-ground organic C as all the organic C except for standing above-ground biomass. Microbial biomass C and N were determined by fumigation–extraction[29].

Plant-microbial ^{15}N partitioning experiment

One aluminium tube (7.2-cm diameter) was installed in each chamber to 20-cm depth on 22 February 1997 and 4.0 mg ^{15}N of $(^{15}NH_4)_2SO_4$, 99.7% atom ^{15}N) were injected on 8 March 1997 in 25 ml of solution. Above-ground plants and soil cores were collected on 23 April 1997. ^{15}N content in shoots, roots and soils were determined on a GC-MS as described above. Microbial biomass ^{15}N ratio was determined after Kjeldahl digestion and diffusion[30]. Sample $\delta^{15}N$ (‰) were converted to excess nitrogen isotope (mg); conversion of $\delta^{15}N$ (‰) to the absolute isotope ratio ($^{15}N/^{14}N$) of the sample was based on the atomic ratio of atmospheric nitrogen. Sample ^{15}N content was then calculated from fractional abundance ($^{15}N/(^{15}N + ^{14}N)$) and total N content of the sample. Non-extractable ^{15}N content (mostly organic ^{15}N) was calculated by subtracting microbial biomass ^{15}N and K_2SO_4-extractable ^{15}N from total soil ^{15}N.

Root and microbial respiration

Field below-ground respiration (BR) was determined using a LI-COR 6200 CO_2 Analyzer (LI-COR, Inc.)[17]. BR was measured in five or six chambers of each treatment with three locations in each chamber. HR in root-free soils was measured as total CO_2 evolution from incubation at 26 °C for 1 day at field moistures or 14 days at constant moisture (20% w/w). The 1-d incubations at field moistures were used to test whether CO_2-improved moistures enhanced HR, whereas the 14-d incubations were to examine the effect of altered C conditions on HR at the constant moisture. CO_2 and C isotope ratios were determined on a GC-MS.

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Regulation of the gain of visually guided smooth-pursuit eye movements by frontal cortex

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In studies of the neural mechanisms giving rise to behaviour, changes in the neural and behavioural responses produced by a given stimulus have been widely reported. This 'gain control' can boost the responses to sensory inputs that are particularly relevant[1–4], select among reflexes for execution by motoneurons[5,6] or emphasize specific movement targets[7]. Gain control is also an integral part of the smooth-pursuit eye movement system[8–13]. One signature of gain control is that a brief perturbation of a stationary target during fixation causes tiny eye movements, whereas the same perturbation of a moving target during the active state of accurate pursuit causes large responses[9]. Here we show that electrical stimulation of the smooth-pursuit eye movement region in the arcuate sulcus of the frontal lobe ('the frontal pursuit area', FPA) mimics the active state of pursuit. Such stimulation enhances the response to a brief perturbation of target motion, regardless of the direction of motion. We postulate that the FPA sets the gain of pursuit, thereby participating in target selection for pursuit.

We studied sites in the periarcuate frontal cortex where electrical stimulation (50 μA) evoked smooth eye movements when monkeys were performing fixation or pursuit. In agreement with previous reports[14,15], these sites were located posterior to and differently from sites where stimulation evoked contraversive saccades. Figure 1a compares the average eye velocity evoked when a 75-ms train of pulses at 333 Hz was applied during fixation of a stationary target and during pursuit of target motion at 20° s^{-1} (continuous traces). In each case, the evoked response is compared to the eye velocity recorded in trials with identical target motion but without electrical stimulation (dashed traces). In the example of Fig. 1a, and at almost all our sites, evoked eye movements were larger when stimulation was delivered during pursuit than during fixation. The latency of the responses was slightly but significantly shorter during pursuit than during fixation (mean ± standard deviation, s.d. is 22.4 ± 3.2 versus 26.8 ± 6.2 ms; paired t-test, $t = 5.3$, 40 degrees of freedom, d.f., $P < 0.0001$).

The polar plots in Figs 1b and c summarize the direction and amplitude of the eye velocity evoked by electrical stimulation during fixation or pursuit at 20° s^{-1}, for 41 sites in 38 penetrations in two monkeys. The length and orientation of each vector indicate the amplitude and direction of the peak value of evoked eye velocity, respectively. During both fixation and pursuit, the direction of the responses at different sites was widely distributed but showed a strong bias toward ipsiversive (same-sided). The size of the evoked eye movement during pursuit was about three times that during fixation (mean ± s.d. is 18.1 ± 8.0 versus 6.2 ± 4.1° s^{-1}; paired t-test, $t = 14.8$, 40 d.f., $P < 0.0001$). However, the direction of the evoked eye movement did not depend strongly on the direction of ongoing pursuit. Regression analysis for the direction of the electrically evoked movement versus the direction of pursuit revealed statistically significant slopes in 10 of 41 sites ($P < 0.05$).

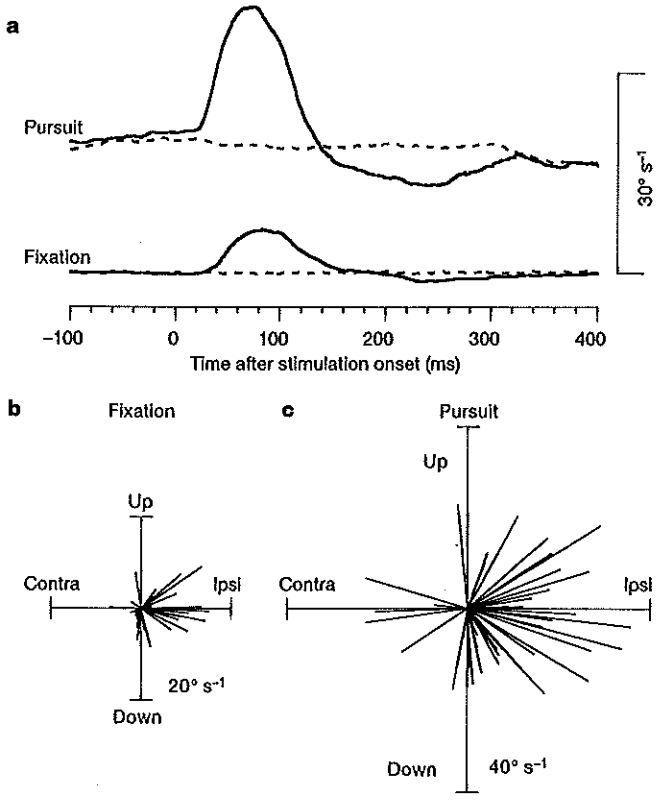

Figure 1 Smooth eye movements evoked by electrical stimulation. **a**, Continuous traces show averages of horizontal eye velocity for trials in which the monkey either fixated a central spot or performed rightward pursuit. Dashed traces show eye movements in non-stimulation controls. In the pursuit task, a stationary target appeared 8° from the centre of the screen for 1,000 to 1,500 ms, then executed step–ramp motion (4° step, 20° s^{-1} ramp) toward the centre of the screen. Polar plots summarizing the direction and amplitude of elicited eye velocity during fixation (**b**) or pursuit (**c**) at all 41 sites tested. For pursuit trials (**c**), electrical stimulation was applied during pursuit in eight directions, and the largest response is shown.