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Transient nature of CO_2 fertilization in Arctic tundra

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THERE has been much debate about the effect of increased atmospheric CO_2 concentrations on plant net primary production[1,3] and on net ecosystem CO_2 flux[3–10]. Apparently conflicting experimental findings could be the result of differences in genetic potential[11–15] and resource availability[16–20], different experimental conditions[21–24] and the fact that many studies have focused on individual components of the system[2,21,25–27] rather than the whole ecosystem. Here we present results of an *in situ* experiment on the response of an intact native ecosystem to elevated CO_2. An undisturbed patch of tussock tundra at Toolik Lake, Alaska, was enclosed in greenhouses in which the CO_2 level, moisture and temperature could be controlled[28], and was subjected to ambient (340 p.p.m.) and elevated (680 p.p.m.) levels of CO_2 and temperature (+4 °C). Air humidity, precipitation and soil water table were maintained at ambient control levels. For a doubled CO_2 level alone, complete homeostasis of the CO_2 flux was re-established within three years, whereas the regions exposed to a combination of higher temperatures and doubled CO_2 showed persistent fertilization effect on net ecosystem carbon sequestration over this time. This difference may be due to enhanced sink activity from the direct effects of higher temperatures on growth[16,29–33] and to indirect effects from enhanced nutrient supply caused by increased mineralization[10,11,19,27,34]. These results indicate that the responses of native ecosystems to elevated CO_2 may not always be positive, and are unlikely to be straightforward. Clearly, CO_2 fertilization effects must always be considered in the context of genetic limitation, resource availability and other such factors.

Net ecosystem carbon balance is the difference between gross primary productivity and losses from plant and soil respiration (together with generally small losses to herbivores). In the historical and recent geological past (Holocene epoch), net primary productivity of permafrost-dominated northern ecosystems often exceeded heterotrophic respiration due to the cold, wet soil environment[34,35]. As a result, these ecosystems during the Holocene were net sinks for carbon with respect to the atmosphere of up to ~0.1 to 0.3 petagrams of carbon per year (Pg C yr^{-1})[34,40].

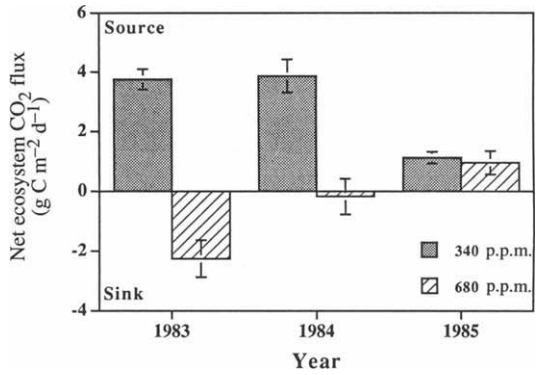

FIG. 1 Seasonal CO_2 flux of tussock tundra (dominated by *Eriophorum vaginatum*) ecosystems exposed to 340 and 680 p.p.m. CO_2 during the 1983–85 growing seasons at Toolik Lake, Alaska. Data are means ±1 standard error; $n = 3$ chambers per treatment.

Recent measurements of CO_2 flux in Arctic ecosystems indicate that tussock and wet sedge tundra are now sources of CO_2 to the atmosphere[34,41,42] possibly due to changes in site water balance[34,40,41,43] following the recently reported increase in northern-latitude surface temperatures[44–48].

Given the huge below-ground carbon stocks in Arctic soils, the release of CO_2 from Arctic ecosystems may exert a positive feedback on atmospheric CO_2 levels and greenhouse warming[41]. Conversely, under conditions of elevated CO_2 and global climate change, northern ecosystems could become a sink for carbon, providing a negative feedback on atmospheric CO_2 levels[34]. The ultimate role of Arctic ecosystems in the global carbon budget largely depends on both the short- and long-term ecosystem response to elevated CO_2 and concomitant climate change.

Higher atmospheric CO_2 has the potential to increase plant growth in a variety of ways, including greater photosynthesis, higher water-use efficiency, depression of respiration, delayed leaf senescence, and relief of nutrient stress via enhanced nutrient-use efficiency, nitrogen fixation and nutrient uptake[3,8,9,16,49]. There is, however, great uncertainty about whether these responses will hold for periods of years in natural

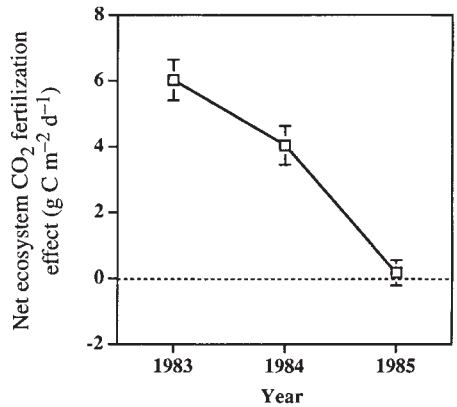

FIG. 2 The CO_2 fertilization effect over three growing seasons at Toolik Lake. Indicated is the absolute stimulation of net ecosystem CO_2 flux by a doubling of atmospheric CO_2 concentration (from 340 to 680 p.p.m.). The CO_2 fertilization effect is calculated as the difference between the flux measured at double and ambient CO_2 levels. Data are means ±1 standard error; $n = 3$ chambers per treatment.

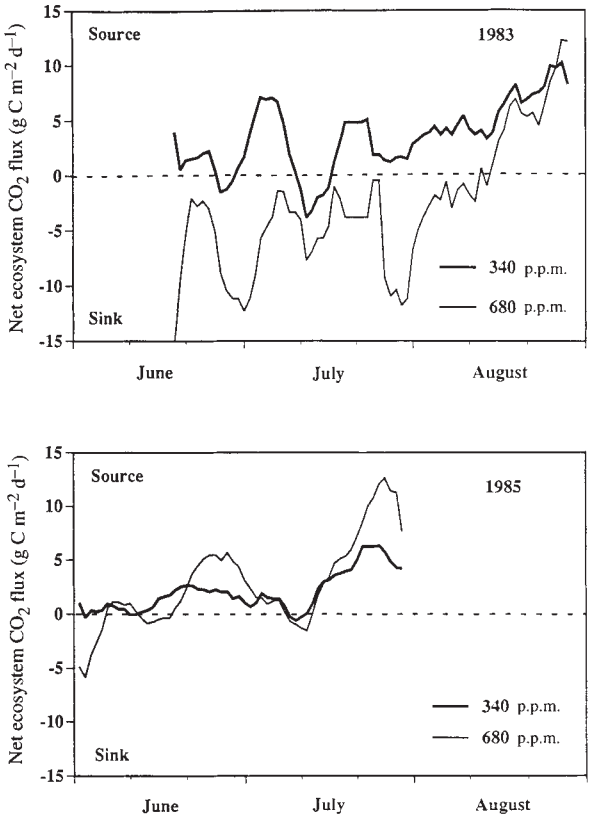

FIG. 3 Daily net ecosystem CO_2 for *in situ* tussock tundra at 340 and 680 p.p.m. CO_2, for 1983 (top) and 1985 (bottom). Data presented are 5-day sliding-mean values calculated from 6-minute average CO_2 fluxes throughout the period indicated. A computer malfunction caused atypically low temperatures for the season, and termination of this phase of the experiment in late July 1985.

ecosystems, and it has been suggested that limitations of water, nutrients and light will prevent most unmanaged ecosystems from exhibiting significant responses to elevated atmospheric CO_2 (refs 7, 10, 34, 50).

Experiments designed to assess the effect of elevated CO_2 on tussock tundra ecosystems (dominated by *Eriophorum vaginatum*) were conducted at Toolik Lake, Alaska (68° 38′ N, 149° 35′ W) between 1983 and 1987[28,41,42,51]. This study was the first *in situ* manipulation of the effects of elevated CO_2 on a natural, unmanaged ecosystem. This fact, and the potential importance of the findings, caused the authors to delay publication of the results until background documents were available in the open literature including the system description[28], contemporary net ecosystem CO_2 fluxes[41] and leaf-level photosynthesis responses[52].

Automated, CO_2- and temperature-controlled greenhouses[28] were used to provide *E. vaginatum*-dominated tussock tundra ecosystems with ambient and elevated CO_2 concentrations during the 1983–85 growing seasons at Toolik Lake. The system consisted of 12 chambers that were 1.2 m square and ~0.5 m tall. The experiment included treatments with three replicates each: ambient CO_2 concentration (340 p.p.m.), elevated CO_2 concentration (680 p.p.m.), and elevated CO_2 concentration plus elevated temperature (680 p.p.m. + 4 °C). Three chamberless plots were used as controls. Net CO_2 flux was measured every 3 minutes, and summed and recorded every 6 minutes. Net seasonal flux was determined as the integral of the seasonal daily fluxes.

Tussock tundra exposed to elevated CO_2 and ambient temperatures exhibited a loss of photosynthetic capacity, whereas plots exposed to both elevated CO_2 and elevated temperature retained the enhanced photosynthetic capacity during the 3-year experiment. Ambient plots were net sources of CO_2 to the atmosphere during all 3 years (Fig. 1). This result has been recently supported in other tussock tundra sites, as well as wet sedge ecosystems on the north slope of Alaska[41,53,54]. Plots exposed to elevated CO_2 were net CO_2 sinks during the first 2 years of exposure; but during the third year of the experiment, such plots were net sources of CO_2 of ~1 g C m^{-2} d^{-1} (Fig. 1).

Despite rapid (within 3 weeks) leaf-level photosynthetic adjustment of the dominant species *E. vaginatum* to elevated CO_2 (ref. 52), the CO_2 fertilization effect during the first year of exposure resulted in significantly greater net ecosystem CO_2 accumulation (Fig. 2). In the first year of treatment, daily net ecosystem CO_2 flux at 680 p.p.m. was stimulated, and positive, from the start of the experiment until late August (Fig. 3). The increase in CO_2 incorporation at the ecosystem level was due to the presence of species that 'down-regulated' photosynthesis or leaf area (for example *Ledum palustre* and *Betula nana*; W.C.O., unpublished data) more slowly than was the case for *E. vaginatum*. Plots exposed to 680 p.p.m. CO_2 accumulated 6 g C m^{-2} d^{-1} more than ambient plots in the first year. However, this fertilization effect decreased in the second year and virtually disappeared in the third year of the experiment. During the second year of CO_2 fertilization, patches exposed to elevated CO_2 accumulated ~4 g C m^{-2} d^{-1} more than ambient plots, but by the third year, the seasonal CO_2 fertilization effect at 680 p.p.m. CO_2 disappeared entirely (Fig. 2). In the third year of treatment, daily fluxes at 680 p.p.m. CO_2 were similar to those at an ambient CO_2 concentration of 340 p.p.m. (Fig. 3).

Plots that were exposed to both elevated CO_2 and elevated temperature were net sinks for atmospheric CO_2 throughout the 3 years of continuous growing-season experimental manipulation (Fig. 4). Presumably elevated temperatures coupled with absolute air humidities and soil water tables enhanced rates of mineralization and nutrient supply and increased potential sink activity, thereby resulting in prolonged stimulation of photosynthesis. Continued enhancement of photosynthesis by elevated CO_2 should require that nutrients are available to support the use of the increased carbohydrate supply in growth or storage[8,9,16,34]. Plant growth and photosynthesis are generally limited by nutrient availability in Arctic ecosystems[55–57]. However, fertilization usually acts to stimulate tissue production rather than to increase leaf photosynthesis[55,56,58]. Carbohydrate supply may actually exceed plant need in Arctic species[52].

Carbohydrate sufficiency in *E. vaginatum* and many other Arctic plants[34,42,52] may explain the rapid ecosystem-level homeostatic adjustment to elevated CO_2 observed here. If carbohydrate use is limited primarily by resource availability, then the sinks for additional carbohydrate produced under conditions of elevated CO_2 will be limited as well[34,52]. Without adequate sinks,

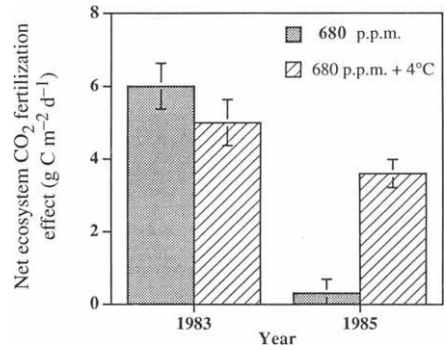

FIG. 4 The CO_2 fertilization effect coupled with a 4 C increase in ambient temperature on net ecosystem CO_2 flux during the first and last year of the 3-year *in situ* elevated CO_2 experiment at Toolik Lake. Shown is the increase in net ecosystem CO_2 flux at 680 p.p.m. CO_2, and at 680 p.p.m. CO_2 and +4 C, compared to ambient (340 p.p.m.) CO_2 and temperature. Data are means ±1 standard error; $n=3$ chambers per treatment.

accumulated carbohydrates may feed back to reduce the amount of Rubisco with a concomitant reduction in photosynthetic potential[25,52].

Northern-latitude warming may lead to greater thaw depth and drainage of upper soil layers[34,41], which would act to enhance soil aeration, decomposition and mineralization[40,59,60]. Increased nutrient availability may have stimulated sink activity and strength in tussock plots exposed to elevated temperature[61–63] allowing for the use of excess carbohydrate reserves, and prolonged photosynthetic response to elevated CO_2 (refs 42, 52).

Increased temperature may also directly increase sink strength and activity, as respiration and growth tend to increase at moderately high temperatures in some Arctic species[56,63,64]. Hence, increased temperatures predicted for northern-latitude ecosystems may directly or indirectly stimulate ecosystem sink strength.

These results indicate that initial stimulation to tussock tundra ecosystems by elevated CO_2 is transient (with homeostatic adjustment) at 680 p.p.m. CO_2, occurring within 3 years of exposure to elevated CO_2. Under current ambient conditions, whole ecosystem respiration is occurring at a greater rate than is ecosystem photosynthesis. Currently high ecosystem respiration rates are most likely due to decreases in site waterlogging[41,53,54] following recently reported temperature increases for northern-latitude ecosystems[44–48]. A concomitant increase in nutrient mineralization should be realized from enhanced soil decomposition[65], which should lead directly to greater plant growth[55,56] and greater ecosystem sink strength for CO_2 (refs 10, 34). Genetic constraints to plant growth, however, may limit the ecosystem response to enhanced nutrient availability[11,14,66]. The potential increase in gross ecosystem productivity, at least in the short term, may not be enough to counteract the increase in whole system respiration.

There are many uncertainties in predicting the long-term effect of global change on Arctic ecosystems. The new equilibrium level of ecosystem productivity, and the resulting carbon balance, will depend on a variety of factors such as plant genetic constraints, plant competition, resource availability and site water balance[16,34,41,52,56,57,67–69]. Over longer time intervals invasion of shrub or tree species may act to increase above-ground carbon storage[34,38,41]. There is currently no evidence that these mechanisms are acting, or will act quickly enough to offset a large net efflux of CO_2 to the atmosphere; it seems likely that significant amounts of carbon will be lost before other factors (including altered vegetation composition) result in re-incorporation of this lost carbon back into Arctic ecosystems or their replacement ecosystems[70].

These results are the first field evidence for complete homeostatic adjustment of CO_2 flux (in a native ecosystem), to elevated atmospheric CO_2, and support conclusions from a variety of sources. This other work includes phytotron experiments on Arctic plants[11], Arctic ecosystem microcosms[68,69] and non-Arctic plants[17,71], greenhouse experiments on a simulated tropical ecosystem[6], and open-top field chamber experiments on grasses[72] and pine trees[27]. These studies all showed little or no 'CO_2 fertilization effect' on plants after some brief period of adjustment. These results sound several cautionary notes for those who feel that elevated atmospheric CO_2 will necessarily lead to increased net ecosystem carbon sequestration[2,73–77]. Clearly, other resources and factors besides CO_2 can limit ecosystem productivity, and therefore potential responses to elevated CO_2. At the same time, CO_2-related climate change can cause a potentially very large release of biospheric CO_2 from terrestrial ecosystems to the atmosphere[41,53,54]

Experiments and observations indicate that warmer temperatures with no change in soil moisture increases can cause a rise in net ecosystem CO_2 uptake[34,38], while warmer and drier conditions may cause a net loss of CO_2 from the ecosystem to the atmosphere[41,53,54]. Knowledge of the effects of interaction of various environmental factors, including elevated CO_2, will be necessary to predict future carbon sequestration and loss by terrestrial ecosystems.

The manipulations reported here were conducted for only three growing seasons. Longer-term experiments or observations are needed to rule out ecosystem response to elevated CO_2 over longer time intervals. This need could be accommodated by longer-term field manipulations, and by field observations of natural CO_2 springs, where plants and ecosystems have experienced long-term exposure (perhaps millennia) to elevated CO_2 (refs 77, 78 and W.C.O., unpublished data). Under these conditions very long-term exposure effects at the ecosystem level, including effects on carbon sequestration, can be evaluated. □

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Climate variations in Europe over the past 140 kyr deduced from rock magnetism

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RAPID shifts in climate during the last glacial are now well documented, particularly from the oxygen isotope records of the two Greenland ice cores GRIP[1,2] and GISP2[3]. In the GRIP record[1,2] these climate events are also seen during the preceding (Eemian) interglacial which may be an analogue for the future climate, warmed by the greenhouse effect. But these shifts are not found in the Eemian section of the GISP2 core[3], casting doubt on whether the rapid shifts in the GRIP oxygen isotope record really do represent a climate signal. Here we present magnetic susceptibility, pollen and organic carbon records from maar lake deposits in the Massif Central, France. These data provide an independent record of past climate and we find that they correlate well with the ice-core records during the last glacial. During the Eemian, two rapid cooling events seen in our record also correlate with those seen in the GRIP ice core, supporting the idea that rapid climate change did occur in the Eemian interglacial and demonstrating that it extended to continental Europe.

In sedimentary deposits, the ferrimagnetic fraction originates from detrital inputs and from authigenic or bacterial production[4]; it is diluted in a mineral or biological diamagnetic matrix and is affected by dissolution[5]. Enhancement and impoverishment processes are influenced by environmental and climate conditions prevailing over the sediment source areas. Magnetic susceptibility is a quick, cheap and non-destructive measure of relative concentrations of magnetic oxides (such as magnetite (Fe_3O_4) and titanomagnetite ($Fe_{3-x}Ti_xO_4$)) and has already contributed to global-change reconstructions from marine[6,7] and loess-palaeosoil sequences[8,9].

Here we discuss sedimentary sequences deposited in maars (phreatomagmatic explosion craters) of the Massif Central, France. Their topographic position and great initial depths favoured a slow but continuous sedimentation over long periods during late Quaternary times. Under cold climate, freeze–thaw alternations stimulated the erosion of the volcanic rocks and the deposition of clastic sediments. Under temperate climate, vegetation and soil development enhanced the organic sedimentation, favouring dilution and dissolution of the magnetic fraction. The magnetic susceptibility is thus strongly sensitive to variations of the local climate and constitutes an accurate proxy record, particularly useful when palaeobiological or organic geochemical information loses some degree of significance (that is, under the coldest conditions).

Lac du Bouchet and Lac St Front lie 40 km apart in the Velay region (45° N, 3° E) at 1,208 and 1,300 m altitude. They are respectively oligotrophic and eutrophic lakes filling subcircular craters less than 2 km wide, cut through Hercynian granites and Quaternary volcanic formations. Several generations of cores have been obtained since 1982; the last provided a 50-m sequence at Lac du Bouchet[10] and a 65-m sequence at Lac St Front. The upper halves of these sequences covering the last climate cycle are treated here. Magnetic susceptibility was initially used as an independent parameter to correlate parallel records of geomagnetic palaeosecular variation[11–16]. Hysteresis cycles, thermomagnetic curves, scanning electron microscope observations and X-ray energy-dispersive spectroscopy microprobe analyses established that euhedral grains of detrital titanomagnetites, 0.1–100 μm in size, are the carriers of he magnetic signal[14,16].

The average susceptibility record of Lac du Bouchet constructed from a first generation of 12 parallel cores (6–20 m long)[11–14] was correlated with the Lac St Front record on the basis of pollen and organic carbon markers (Fig. 1). Granulometry, heavy mineral determination, clay mineralogy[17], organic geochemistry[17–19] and diatom analyses[20] independently supplied information on sedimentary environments. The two endmember sediment types are: (1) silty clays supplied by cryoclastic erosion of volcanic rocks under cold climate (susceptibility $>400\times10^{-8}$ m^3 kg^{-1}); (2) organic gyttjas formed under temperate climate by autochtonous organic matter and soil degradation products (susceptibility $<200\times10^{-8}$ m^3 kg^{-1}). Arboreal pollen percentage[21,22] and temperature variations reconstructed by transfer functions on pollen assemblages[23] provide a local climate record comparable with the susceptibility record (Fig. 1*a–c*). A strong negative correlation ($-0.8<r<-0.7$) is due to the simultaneity of large amplitude changes recorded at boundaries of climate events. It confirms the climatic significance of the susceptibility record deduced from the simple model introduced above.

The susceptibility record along its original timescale (see Fig. 2 for the depth-to-time transformation) was compared with the most detailed continental climate record available for the last climate cycle: the $\delta^{18}O$ record from the GRIP ice core (Summit, Greenland)[1,2] (Fig. 3). Susceptibility features and $\delta^{18}O$ cycles (termed Dansgaard–Oeschger events[2]) present the same wavelengths and similar general shapes. Considering the uncertainties of the chronologies (see refs 24, 25 and Fig. 2) we felt justified in performing slight realignments, in order to improve the corre-