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COMPARING STUDIES OF ARTIFICIAL AND NATURAL ECOSYSTEM RESPONSES TO CO_2 ENRICHMENT

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JONES T. H., BEZEMER T. M., KÖRNER C., LAWTON J. H. and THOMPSON L. J. *Comparing studies of artificial and natural ecosystem responses to CO_2 enrichment.* BIOTRONICS **29**, 1–7, 2000. Can experimental investigations of complex systems provide a clearer basis on which to make predictions about the real world? Can model ecosystems predict, at least qualitatively, natural effects? Using two superficially very different grassland ecosystems (natural alpine grassland and grassland model ecosystems) the effects of elevated atmospheric carbon dioxide (CO_2) on these systems are compared. Although very different in composition, climatic conditions and successional stage, results from the two experiments show considerable similarities. Both experiments also highlight the implications for long–term feedback processes in soil ecosystems that are subject to rising global atmospheric CO_2 concentrations. Finally, while studies show that small–scale, short–term single species experiments can yield misleading results we advocate the use of either field manipulations of real ecosystems or, if this is not possible for reasons of cost or time, more realistic (and complex) model systems (microcosms).

Key words: elevated CO_2; climate change; ecosystem processes; model ecosystems; controlled environment facilities

INTRODUCTION

We know that atmospheric carbon dioxide (CO_2) concentrations are increasing through human activities, and we can make relatively good predictions of the levels we can expect to see in the near future. The ecological effects of this rising CO_2 are not as easy to predict. Ecologists are constantly

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being asked to make predictions at the community, ecosystem and biosphere level using information from lower levels (e.g. individual species) (*22*). There are numerous reasons why this is a difficult task. For example, (i) CO_2-enrichment studies are frequently conducted with a free mineral nutrient supply that is not very relevant to natural vegetation. (ii) While pot experiments have contributed greatly to our understanding of how individual plants may respond to various treatments, many responses are altered when multi-species interactions come into play – biological isolation is rare in the real world. (iii) In many cases, long-term effects have not been studied; a full life-cycle (generation) represents a useful experimental duration (*10*). Can experimental investigations of more complex systems provide us with clearer bases on which to make predictions about the real world?

In this paper, we compare and contrast the results obtained from two recently published studies investigating the effects of elevated CO_2 on two superficially very different grassland ecosystems. The first is a natural alpine grassland at 2,470 m altitude in the Swiss Central Alps exposed to elevated CO_2 by using open top chambers (*13*); the second used grassland model ecosystems maintained in the Ecotron controlled environment facility at the Natural Environment Research Council (NERC) Centre for Population Biology at Silwood Park (*14, 8*). We chose these two "extremes" as being representative of "natural" and "artificial" ecosystem approaches to global climate change studies. We ask whether model ecosystems can predict, at least qualitatively, the consequences of enhanced atmospheric CO_2 in natural systems.

DESCRIPTIONS OF SYSTEMS

Details of both ecosystems are given in the respective papers; here we summarise the salient features.

Alpine grassland

Experiments were conducted at 200–300 m above the climatic tree-line in a sedge-dominated alpine turf (*Caricetum curvulae*) near the Furk Pass in the Swiss Central Alps (47°N). Soils are deeply weathered acid (pH 4) gleyic podzo-cambisols on glacial moraines and are strongly enriched with aeloic sediments. Mean mid-summer air temperatures vary between 7 and 10°C, but canopy temperatures regularly exceed 20°C under direct solar radiation. *Carex curvula* represents about 62% of the total above-ground biomass, *Leontodon helveticus* represents 11%, other herbs (e.g. species of *Potentilla, Phyteuma, Trifolium*) account for 25%. The remaining 2% is composed of various grass species including *Poa alpina* (see *13*).

Cylindrical open top chambers made of UV-transparent Plexiglass (37 cm diameter and height, enclosing roughly 500 tillers of *C. curvula*) were placed on each of 32 plots. Sixteen plots received air with 680 μmol mol^{-1} CO_2, and 16 received ambient air (ca. 355 μmol mol^{-1}). Treatments began with snow-melt in 1992 and ended with the 1995 harvest conducted shortly after the time of the seasonal biomass peak at 10–12 August. (For more details see *13, 19, 20*).

Ecotron model grassland

The experiment used 16 model ecosystems, each $1 m^2$, maintained in the Ecotron controlled environment facility. Temperature, humidity, light and water were computer–controlled and a 24 h diurnal pattern without seasonality was maintained. Rainfall (reverse osmosis water) was delivered from an irrigation lance situated above the soil surface. One minute long irrigations each delivering 4.21 of water occurred three times per day. Eight chambers were maintained at ambient external atmospheric CO_2 concentrations, which fluctuated naturally between 350 and 400 μmol mol^{-1}, and eight were dynamically maintained at 200 μmol mol^{-1} above ambient.

Soil was fumigated using methyl bromide and the soil profile consisted of $0.1 m^3$ gravel topped with $0.3 m^3$ of 40 : 60 sand : Surrey loam mix placed in 0.4 m^3 containers. Each container received 120 ml of a standard microbial inoculum prepared from a 20–25 μm pore filtrate (Whatman No. 4) of Silwood Park soil. This treatment also introduced protists and nematodes to all chambers.

The community, established in the soil, consisted of primary producers, herbivores, secondary consumers (parasitoids) and soil micro– and macro–organisms. Four species of plants were used : *Cardamine hirsuta, Poa annua, Spergula arvensis* and *Senecio vulgaris.* Over three generations, all communities became dominated by *P. annua.* An artificial 'winter' was imposed by cutting most of the above–ground vegetation at the end of each generation and replacing it immediately as litter. All chambers were initiated with the same community and several ecosystem processes were measured over three plant generations. (For more details see *3, 8, 9.*)

COMPARISON OF RESULTS

We consider six ecosystem parameters that were measured in both systems : (i) Biomass responses (plant and microbial) ; (ii) Gas exchange ; (iii) Fate of excess carbon under elevated CO_2 ; (iv) Soil microbial responses ; (v) Plant tissue responses ; and (vi) Decomposition. Rather than repeat information already presented in detail in other publications, here we only summarise the significant results (with the corresponding reference). Table 1 brings together the general pattern of response for each ecosystem property or process and, where appropriate, indicates the direction of that response, for both systems. Note that we are interested only in general response directions and not specific quantitative comparisons.

DISCUSSION

Although very different in composition, geographical location, climatic conditions and successional stage, results from the two experiments show interesting similarities. Other than significant differences in above–ground plant

Table 1. General pattern of response for six ecosystem parameters measured in both Swiss alpine grassland and grassland model ecosystems. References refer to primary publication of research and data.

Parameter	Swiss Alpine Grassland	Ecotron Model Grassland
Biomass: above-ground	No above-ground biomass simulation. Elevated CO_2 had no effect on individual species biomass. (*19, 20*)	No marked increases in total above-ground biomass in elevated CO_2. Significant species- and generation-dependent effects. (*4, 8*)
Biomass: root and rhizome	Total root and rhizome biomass in the uppermost 10 cm greater in plots maintained at high CO_2. (*13*)	Significant treatment effects in root dry weights in the top layer (0–10 cm) in elevated CO_2; higher after 4.5 months, lower after 9 months. (*9*)
Biomass: microbial	Elevated CO_2 had no effects on microbial biomass. (*13*)	Soil microbial biomass unaffected by elevated CO_2. No consistent treatment differences in bacterial taxonomic composition. Fungal taxonomic composition differed between treatments. (*8, 9*)
Gas exchange: CO_2 uptake	Net ecosystem CO_2 uptake was 41% higher during peak mid-season midday hours of Year 2, in Year 3 a full season carbon balance indicated a surplus of carbon of 22%. In Year 4 there was still a stimulation of CO_2 uptake at the beginning of the season, but the signal disappeared by mid-season. (*5, 13*)	Communities growing in elevated CO_2 fixed more carbon (10–17%) for most of the three plant generations. (*8*)
Fate of excess carbon in elevated CO_2	Increases in soil organic matter or allocation of dissolved organic matter into deeper soil horizons likely. Changes in soil pools impossible to detect. Results suggest that carbon was transferred to the soil carbon pool (*13*)	Soil concentrations of dissolved organic carbon (DOC) were higher in elevated CO_2. (*8*)
Soil microbial responses: enzymatic activity	Soil cellulase activity measured at harvest was significantly higher. Screening tests for *in vitro* substrate utilization revealed various changes in degradative abilities of the microflora, indicating altered substrate availabilities. (*13*, Insam *et al.* unpublished in *13*)	One fungal functional group, cellulose decomposers, had higher biomass in elevated CO_2. No major treatment effects recorded for urease, xylanase, trehalase and arginine deaminase. (*8, 9*)
Plant tissue response: above-ground	N- and C-contents were consistently increased under elevated CO_2, but differences were more pronounced in forbs than in graminoids. (*20*)	Leaf C- and N-contents unaffected by CO_2 treatment. (*4*)
Plant tissue response: roots	Composition of below-ground tissues showed no changes under elevated CO_2. (*20*)	No change in root C : N ratios between treatments during the course of the experiment. (*9*)
Decomposition	No long-term litter accumulation but reduced decomposition of litter produced under elevated CO_2. (*1, 6*)	Increased decomposition rates of cotton strips placed in soil under elevated CO_2 conditions. (*8*) (Unpublished data show similar reduced decomposition rates in litter produced under elevated CO_2.)

tissue C– and N–contents, and decomposition rates, the patterns observed are qualitatively similar from both Swiss Alps and Ecotron grassland ecosystems. For the two variables where differences are found, neither is surprising; plants are known to respond species–specifically to elevated CO_2 (e.g. *7*), and rates of decomposition in the two studies were evaluated on two different materials (plant litter *vs*. cotton–strip).

There is a general discrepancy common to both studies between C–assimilation (whole ecosystem C–assimilation was strongly stimulated in both the Alpine and Ecotron grasslands, and canopy photosynthesis measurements showed individual species assimilating more carbon in elevated CO_2) and C–accumulation in above–ground biomass (which hardly changed in either study). These results are similar to findings in other CO_2 enrichment projects (e.g. *2, 11, 15, 16, 17, 18, 23*) where enhancement has yielded only marginally, and often not significant, effects on overall community above–ground biomass. What is also apparent from both studies is that any significant differences that do occur in plant populations in elevated CO_2 are species–dependent.

Both experiments also highlight, to varying degrees of detail and with different evidence, the implications for long–term feedback processes in soil ecosystems that are subject to rising global atmospheric CO_2 concentrations. Both ecosystems point to potential increases in root biomass in high CO_2 conditions (although the direction of this change varied across plant generations in the Ecotron system (*8*)) and significant changes in soil processes. In the Ecotron it would appear that increases in photosynthetically fixed carbon were allocated below ground, raising concentrations of dissolved organic carbon in the soil. These effects were then transmitted up the decomposer food chain. Soil microbial biomass remained unaffected, but the composition of the soil fungal species changed, with increases in rates of cellulose decomposition. In this context, we also observe the increased cellulase activity in the Swiss grassland. In the Ecotron, there were also changes in the abundance and species–composition of Collembola, fungi–feeding arthropods.

That two such different study sites yield broadly similar messages about the impacts of elevated CO_2 on multi–species, interacting communities implies that it may be possible to adopt a more comparative approach, using complex intact ecosystems, to make general predictions about the ecological effects of rising atmospheric CO_2 concentrations. Sufficient studies have now shown that highly reductionist investigations on single, or small numbers of species, for relatively short periods of time, be they on plants or insects (*2, 10, 22, 4*), are unlikely to provide adequate predictions of the effects of climate change on more natural complex systems. Ecosystem interactions and feed–backs (missing from simple experimental systems (see *22*), involving fungi, bacteria, meso–fauna, herbivores, nutrients and water become subject to both direct and indirect effects of CO_2, leading to complex spatially and temporally variable effects. We advise that further experiments designed to predict the effects of enhanced CO_2 on whole communities and ecosystems should abandon the use of small–scale, short–term single species experiments and instead, go either directly to field manipulation of real ecosystems (*21, 12*), or if this is not possible for reasons of cost or time, to more realistic (and complex) model systems (*10, 22, 14*). We believe that it is only by adopting this approach and experimentally manipulating whole ecosystems from contrasting environments that we can even begin to hope to gain consensus about the potential outcome of the current 'experiment' humans are conducting with the entire biosphere.

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