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Biotic carbon feedbacks in a materially-closed soil-vegetation-atmosphere system

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Abstract

Materially-closed, energetically-open biological systems are ideal for investigating biotic feedbacks as they allow for a simultaneous two-way feedback loop between the biotic and abiotic components to take place. However, they have been avoided in ecological research due to the challenge of achieving sustainable and sealed model systems. Here we show that using *pro rata* amounts for the main terrestrial carbon (C) pools allows for the establishment of a system with balanced the autotrophic and heterotrophic C fluxes. Such systems are sufficiently stable to allow for an investigation of biotic C feedbacks. Using this approach, we tested an alternative way of assessing the impact of elevated CO₂ and temperature on the biotic C feedbacks in a materially closed Soil-Vegetation-Atmosphere System (mcSVAS). The results suggest that without nutrient and water limitation, the short-term biotic responses of the SVASs could potentially buffer a temperature increase of 2.3°C without significant positive feedbacks to atmospheric CO₂. Whilst representing a simplified version of land C dynamics, such closed system research represents an important new form of an *in situ* test-bed and model validation of plant and soil biotic responses to environmental changes.

A major uncertainty in predicting future atmospheric CO₂ concentrations and temperatures, second only to the uncertainty in predicting future anthropogenic emissions, is the magnitude and sign of terrestrial carbon (C) feedbacks (3). Realistic parameterisation of the plant and soil feedbacks to environmental change lies at the heart of land C models, but despite recent improvements in modelling, uncertainty

remains large because many aspects of the soil-vegetation-atmosphere interactions are poorly understood (4).

An alternative and complementary, yet underexplored approach to investigate the impact of biotic feedbacks on the C cycle is to use physical analogues setup in materially-closed, energetically-open systems. Materially-closed systems are well suited and relevant to study biotic C responses to climate change. The ability to form and sustain bi-directional feedback loop between biotic and abiotic components is inherent to closed systems only and cannot be observed when materially open approaches. Furthermore, close system approaches are ideal for mass balance studies, but also for detecting subtle feedbacks. The element of closure allows for an accumulation of substances which would normally be beyond the resolution of conventional materially open experimental approaches (Nelson, et al. 2003b, Dempster 2008).

In the research described in this paper, we set out to construct simplified materially closed but energetically open Soil-Vegetation-Atmosphere Systems (mcSVASs) to estimate the plant and soil feedbacks to elevated CO₂ and temperature. Such an approach has often been avoided in ecological research, mainly due to the difficulty of achieving total closure, whilst also balancing the autotrophic and heterotrophic fluxes and hence achieving sustainable model systems. To date, the only attempt to establish an analogue materially-closed model system of the biosphere (Biosphere 2) (10) indicated the severe consequences of failing to appropriately control the atmospheric CO₂ concentrations through managing and representing correctly the major C reservoirs. Our mcSVASs were setup with scaled-down C pools of best estimates of pre-industrial global terrestrial C in soil, plant and atmosphere. Preliminary

runs aimed at exploring the importance of the C stocks for achieving stable systems showed that recreating the *pro rata* C stocks of the terrestrial C cycle represents an important starting point (Supplementary Fig 1) for balancing the autotrophic and heterotrophic C fluxes. This was achieved by setting the initial atmospheric concentration of CO₂ to ~ 280 p.p.m.v. with corresponding *pro rata* plant and soil C stocks, thus creating an analogue system consisting of the pre-industrial global atmospheric (560 Gt C), vegetation (900 Gt C) and soil (2011 Gt C) C pools, falling within the upper range of available global C estimates (12, 13).

The mcSVASs were established in fifteen transparent growth chambers (with an internal volume of 120 l) using state-of-the-art glove-box technology to ensure a materially closed environment (Fig.1), and each was housed within an individual and climate controlled walk-in growth chamber (11). The design enabled non-invasive monitoring and control of temperature and atmospheric CO₂ concentrations with external control of photosynthetically active radiation following a day-night regime of 14-10 h (see materials and methods for more details). All units were initially maintained isothermally at 15°C ± 0.2 s.e.m., a temperature close to the estimated pre-industrial global average temperature of 13.7°C (1). Subsequently, three treatments with five replicated mcSVASs (i.e. n = 5) used in each scenario, were performed in order to assess the plant and soil biotic C feedbacks to elevated CO₂ and temperature. These were: **(i)** a control treatment with no CO₂ additions and no climate sensitivity (isothermal 15°C), hereafter referred to as the control scenario (S₁₅); **(ii)** a scenario with simulated CO₂ additions (18p.p.m.v. CO₂ every second day, equivalent of the IPCC B1 scenario of ~ 930 Gt C cumulative by year 2100) (16) and no climate sensitivity (isothermal 15°C), hereafter referred to as the CO₂ addition scenario (S_{15CO2}); and **(iii)**

a scenario with the same simulated CO₂ additions as in (ii), but with emulated temperature sensitivity to CO₂, hereafter referred to as the emissions with feedback scenario (S_{Δ3CO2}). As the atmospheric CO₂ concentration rose or fell in this treatment, an accurate internal CO₂-temperature feedback control ($\pm 0.2^{\circ}\text{C}$ s.e.m.) enabled the temperature within the mcSVASs to be externally regulated (increased or decreased accordingly). Temperatures were adjusted according to a temperature sensitivity to CO₂, based on the most likely ‘climate sensitivity’ of 3°C (1, 14), defined as the equilibrium response of global mean temperature to doubling the atmospheric CO₂ concentration (ΔT_2) (15).

Results and discussion

The C mass balance analysis performed at the end of the experiment indicates that mcSVASs were successful in conserving the initially introduced C dynamics (Table 1). Similar to the trial runs (Supplementary Fig. S1), two weeks following chamber closure, the mcSVASs with the S₁₅ scenario showed stabilised net C flux dynamics, i.e. the weekly slope of atmospheric CO₂ change was not different from zero (Table S1, Fig. 2A, B) and the atmospheric CO₂ concentrations showed a strong diurnal pattern, driven by the presence or absence of light. In the S_{15CO2} and S_{Δ3CO2} treatments, despite an initial increase in the atmospheric CO₂ content, the atmospheric CO₂ concentration also stabilised at just below 500 p.p.m.v. starting with the experimental week 7 (Fig. 2A, B, Table S1). Furthermore, the stabilisation of the atmospheric CO₂ concentration in the S_{Δ3CO2} treatment took place despite a temperature increase of 2.3°C and was just marginally but not significantly higher than in the S_{15CO2} treatment. The increase in temperature in the S_{Δ3CO2} treatment led to higher total (plant and soil) dark respiration of

the mcSVASs, but only after seven weeks of CO₂ additions and temperature increase; the temperature sensitivity of the dark respiration (Q_{10}) was around 2. In contrast, in the S_{15CO2} treatment the dark respiration was not different from the control (Fig 2C). The stabilisation of atmospheric CO₂ concentration in the S_{15CO2} and S_{Δ3CO2} treatments was explained by the significantly higher plant CO₂ uptake relative to the S₁₅ treatment after five weeks (Fig. 2D, Table S1). Furthermore, CO₂ uptake in the S_{Δ3CO2} scenario was significantly higher than in the S_{15CO2} (Fig. 2D, Table S1). Despite enhanced total dark respiration in the S_{Δ3CO2} treatment (Fig. 2C), the enhancement of CO₂ uptake via photosynthesis (Fig. 2D, table S2) lead to the removal of 62% of the total injected atmospheric C and limited the gain in atmospheric CO₂ in the S_{Δ3CO2} relative to the S_{15CO2} treatment to only 6%. If up-scaled to the Gt C unit used as a reference for the establishment of the *pro rata* C pools in the mcSVASs, the observed sensitivity to CO₂ (i.e. the change in C uptake per atmospheric CO₂ increase estimated from the experimental weeks 7-9) was equivalent to 2.43 Gt C/p.p.m.v. CO₂. The sensitivity of the mcSVASs to the imposed temperature increase (i.e. the change in net C uptake per °C increase) indirectly estimated from the difference between the average weekly slope of CO₂ increase in the S_{Δ3CO2} and S_{15CO2}, was -20 Gt C/°C.

The capacity of the systems to recover after the cessation of ‘emissions’ was examined towards the end of the experiment when the CO₂ addition was stopped after 31 injections, two months after the first CO₂ addition. Halting CO₂ additions made apparent the size of the system’s C sink in the S_{15CO2} and S_{Δ3CO2} scenarios (Fig. 2B; Table S2). Interestingly, the recovery of atmospheric CO₂ was, however, not complete and the temperature-disturbed systems showed a retained memory of the perturbation in gross fluxes (Figs. 2A, B).

Our materially-closed systems, although simplistic, provide several important insights. Firstly, using pro rata amount of C for the main terrestrial pools it is possible to establish sustainable materially closed systems where the autotrophic and heterotrophic C fluxes are balanced, long enough to make the approach feasible for investigating biotic C feedbacks. Secondly, we found a strong plant-driven negative feedback on atmospheric CO₂ — i.e. the stimulation of photosynthesis by elevated CO₂ was increased by 33.8% in the S₁₅CO₂. This is accompanied by an increase in dry weight plant biomass of 22.5% at the end of the experiment (Table 1), values which are within the upper range of CO₂ fertilisation rates for forbs^{\$\$}.

Furthermore, in the S_{Δ3}CO₂ treatment where the temperature increased by up to 2.3°C as it was adjusted depending on the CO₂ concentration, the photosynthetic rate increased by 64.1% (and the plant biomass by 35.6% relative to the S₁₅ treatment) preventing a switch of the mcSVASs from a net C sink to C source. Relative to the S₁₅CO₂ treatment this is an increase of 22.7%, equivalent to ~ 9.9% per °C. This additional increase in C uptake in the S_{Δ3}CO₂ treatment indicates an interactive effect of increasing CO₂ concentration and temperature. Although the review studies concerning the interactive effect of increasing CO₂ and temperature on plant growth found little evidence of large differences in response to CO₂ at different temperatures due to multiple confounding factors (Morison & Lawlor, 1999), there is a strong theoretical basis for expecting interactions between CO₂ and temperature effects on photosynthesis^{\$\$}, which has been revealed by experimental research and supported by a strong, mechanistic framework.

The results from our mcSVATs suggest that without nutrient and water limitations, the short-term biotic responses of a SVAT system could potentially buffer a temperature increase of 2.3°C without significant positive respiration feedbacks to the atmospheric CO₂. However, we recognise that our model systems are simplistic and several caveats need to be pointed out. The experimental time may be too short to include potential acclimation responses to elevated CO₂ and temperature, especially where frequent injection of CO₂ was used to simulate anthropogenic emissions. Additionally, the systems were not nitrogen or water limited. Both of these compounds are known to constrain soil and plant responses to elevated CO₂ and temperature. In addition, the model plant we used is a herbaceous species, whose photosynthetic stimulation by elevated CO₂ is generally considered to be lower than that of trees (24), but higher than that of C4 plants (Ehleringer *et al* 1991).

However, in a physical analogue there is no need to digitally parameterise key processes such as soil Q₁₀s and plant CO₂ uptake. In addition, it is worth noting that computer models can only parameterise feedbacks that are well understood and quantified. In contrast, any unknown plant or soil feedbacks will still inherently take place in physical models if the scale of representation allows; to our knowledge the parameterisation of the CO₂ fertilisation effect has never been derived from analogue systems where the plant response directly impacts on the ambient CO₂ concentration and temperature, which in turn is known to feed back on the photosynthesis rate. The results from our materially closed approach indicate the urgent need to better understand the biotic controls and feedbacks in the global climate system. Whilst the materially closed approach has been so far avoided in ecological research due to its multiple challenges, we argue that it has the potential to uncover key properties of the processes

that drive global biotic feedbacks which will ultimately help to predict future Earth system changes using C-cycle coupled general circulation models with more certainty. Indeed, the construction of mcSVASs incorporating elements of global biotic and climatic heterogeneity represents a major, but achievable, challenge. These enhancements would increase the realism of the mcSAVSs and enable further insights into the mechanisms controlling the global C cycle.

Materials and methods

Materially-closed, energetically-open SVASs. Transparent chambers manufactured from welded polycarbonate (10 mm wall thickness and 120 l volume, Supplementary Fig. S1) were setup within the Ecotron facility at Silwood Park (26). Each chamber was connected to a separate measuring cell mounted under a rotating open-path infra-red gas analyser (OP-2 Open Path CO₂/ H₂O Analyser, ADC Bioscientific Ltd., Herts, UK), allowing non-invasive and continuous real time air CO₂ concentration measurements (11). Temperature, atmospheric pressure, RH, O₂ concentration, soil moisture and PAR were continuously measured and recorded by the TREND 963 data logging supervisor (Trend Control Systems Ltd., Horsham, UK). The temperature was controlled by continuously operating a heater and a chiller, both integrated within each EAC. The moisture content of the soil/sand mixture was monitored by a soil moisture probe (Theta Probe, Delta-T Devices Ltd., Cambridge, UK) and homeostatically maintained between 35-60% by triggering watering events of ~ 20 ml of water from an internal reservoir of 280 ml each time the soil moisture dropped below 35%.

Leakage estimates. Although the chambers were constructed to full anaerobic gas chamber standards, maintaining perfectly materially closed systems over the course of

the long-term experiments is a major engineering challenge. Internal and external pressure changes were used to calculate the volume of air which was exchanged with the outside environment over the course of the experiments using the combined ideal gas law. Continuous CO₂ recordings in- and outside the boxes allowed for the calculation of the amount of C exchange and net contamination for each experimental unit over the course of the experiments (0.00003 ± 0.00017 g C s.e.m). The net deviation from the targeted C amounts at the end of the experiment was below 4% (Table 1) and was most likely introduced during the experimental setup as it is intrinsically difficult to introduce precise C amounts as living vegetation.

Biological components. We aimed to match pre-industrial ratios of soils, terrestrial vegetation, and atmospheric carbon (Table 1). 2.85 g of dry arable soil (2.13% C, 0.16% N) was used together with 0.528 g FW (14% DW, 38% C DW, 1.85% N DW) of the C₃ plant *Pilea glauca* (Urticaceae). Selected after screening a total of eight plant species *P. glauca* was selected as the experimental plant species because of its slow growth rate and known suitability as a durable species in ‘bottle gardens’. A carbon-free sand (550 g, <0.001% C, <0.01% N) was used as additional inert matrix for plant roots. External lighting was provided by a mixture of halogen and fluorescent tubes with PAR adequate for this understory plant species ($120 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Statistical analysis. All mcSVASs had independent temperature control and were consequently treated as true replicates. The R statistical package (version 2.7.1) was used to perform repeated measure ANOVA on the effects of temperature treatments on the weekly slope of CO₂ concentration and the weekly CO₂ uptake (photosynthesis) and release (night-time respiration) rates. Individual ANOVAs followed by contrast analysis

were performed for each week to test if the response of the treatments including elevated temperature and CO₂-temperature feedbacks differed from the control.

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Figure legends.

Fig. 1. Photograph of one materially-closed Terrestrial Analogue Chamber (TAC). **(A)** Plant (*Pilea glauca*). **(B)** Pot containing carbon free sand and soil. **(C)** Soil moisture probe. **(D)** Light (PAR) sensor. **(E)** Pressure and temperature sensors. **(F)** Heater. **(G)** Chiller. **(H)** Water reservoir. **(I)** Peristaltic irrigation pump. **(J)** Air pump providing continuous air circulation between TACs and the open-path infrared gas analyser. **(K)** Fans maintaining continuous internal air mixing.

Fig. 2. Atmospheric CO₂ concentrations, slopes of CO₂ concentration change, daily magnitudes of CO₂ release (respiration) and uptake (photosynthesis) in the earth analogue chambers (TACs) for the isothermal 15°C (S15), isothermal 15°C + CO₂ additions (S_{15CO2}) and CO₂ additions + feedback $\Delta T_2=3$ (S _{$\Delta 3$ CO2}) scenarios (n = 5). **(A)** Average atmospheric CO₂ concentrations and average temperature changes for the different periods of the experiment. CO₂ emissions were simulated by injecting a constant amount of pure CO₂ calculated to result in a 15 p.p.m.v. CO₂ increase every second day. The temperature in the EACs which included the CO₂ temperature feedback was externally adjusted every second day (between CO₂ injections) as a function of the atmospheric CO₂ concentration, assuming a climate sensitivity of 3°C. **(B)** Average daily slope of CO₂ concentration change ($\pm$ s.e.m.) for the different periods of this experiment. The ‘recovery phase’ represents the last 16 days of the experiment after the cessation of the CO₂ additions. **(C)** Average daily rate of CO₂ release (night-time

respiration $\pm$ s.e.m.) for the different periods of the experiment. **(D)** Average daily rate of CO₂ uptake (photosynthesis $\pm$ s.e.m.) for the different periods of the experiment.

Table 1. Carbon (C) mass balance comparing the initial amounts of C in the main pools with those found at the end of the experiment in the isothermal 15°C (S₁₅), isothermal 15°C + CO₂ additions (S_{15CO2}) and CO₂ additions + feedback $\Delta T_2=3$ (S _{$\Delta 3$ CO2}) scenarios within each mcSVAS treatment (n = 5).

Time of measurement	Initial C amounts (g)	C amounts (g) at the end of the experiment for each temperature treatment		
Source/Scenario		S ₁₅	S _{15CO2}	S _{$\Delta 3$CO2}
Air	0.0172	0.0183 ± 0.002	0.0253 ± 0.003	0.0260 ± 0.003
CO ₂ Emissions	na	na	0.03	0.03
Plant	0.0400	0.0620 ± 0.004	0.0760 ± 0.07	0.0841 ± 0.07
Soil	0.0710	0.0505 ± 0.003	0.0510 ± 0.001	0.0510 ± 0.003
Contamination	na	0.0008	0.0001	<0.0001
Total	0.1282	0.1315 ± 0.006	0.1523 ± 0.003	0.1609 ± 0.004
Unexplained	na	0.0049	-0.0059	0.0027

Figure 1

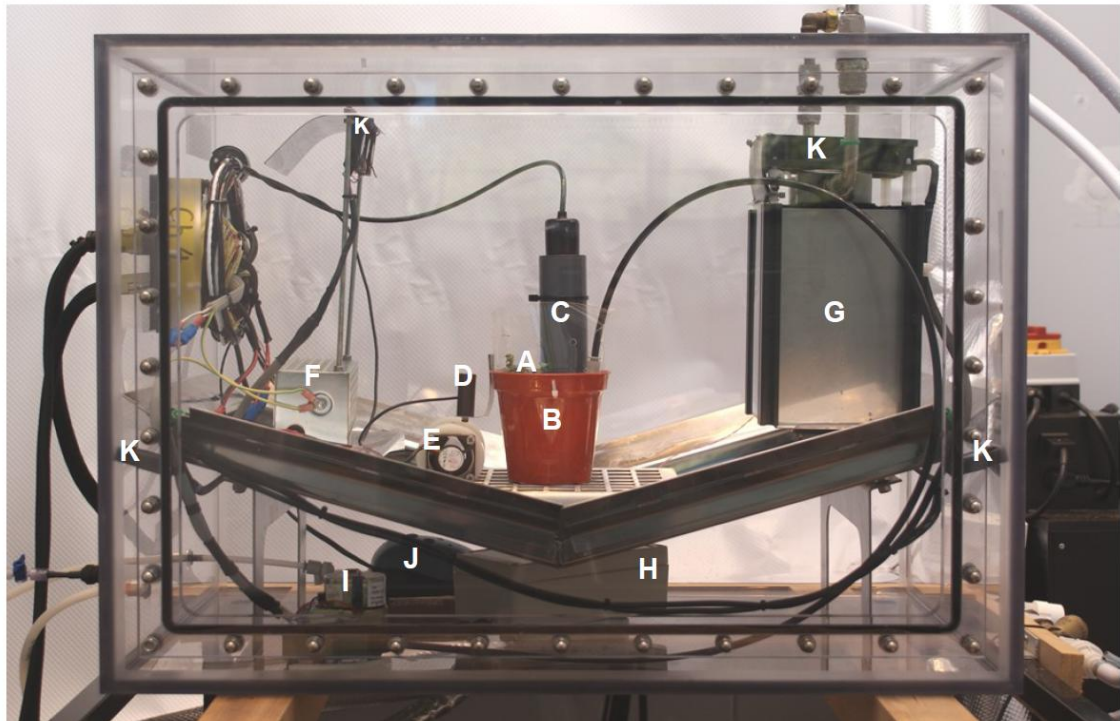
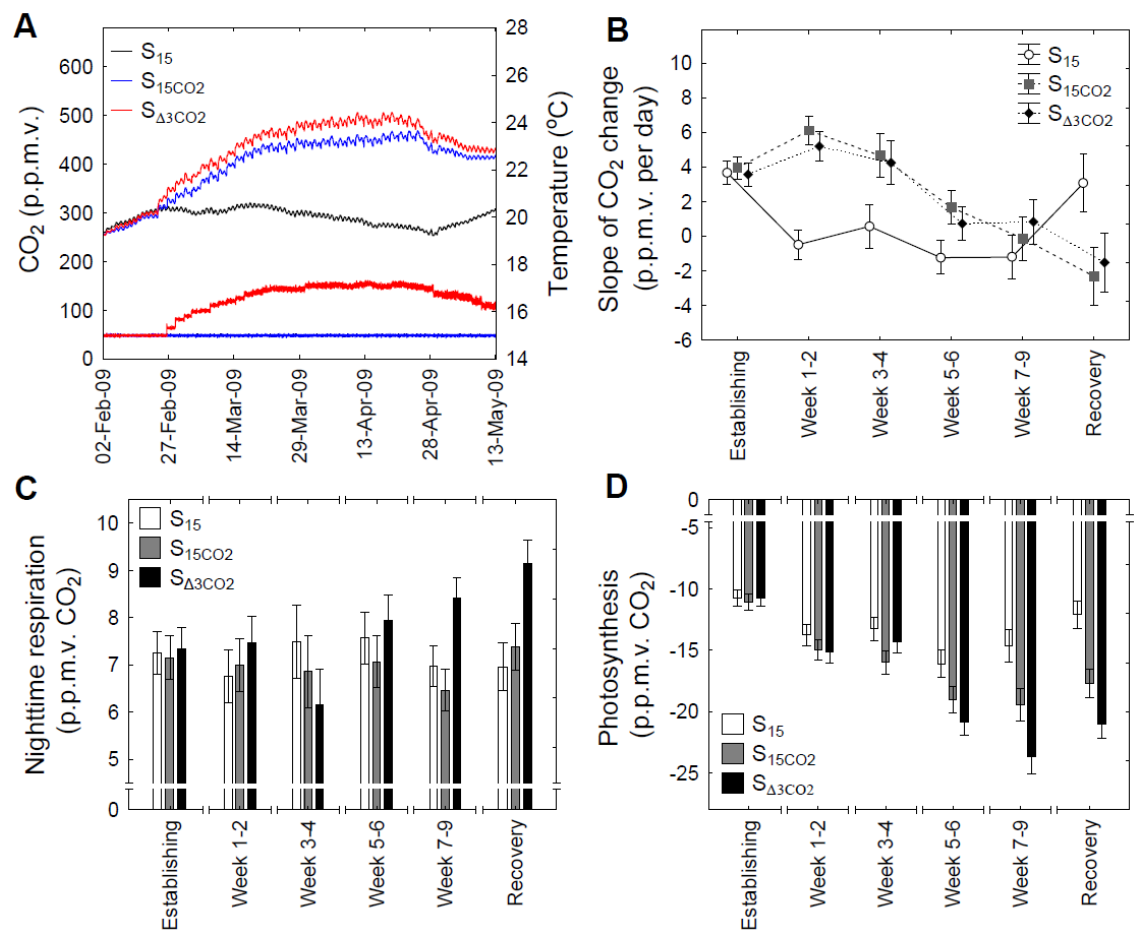


Figure 2



Supplementary Figure S1

