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Elevated CO₂ maintains grassland net carbon uptake under a future heat and drought extreme

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Extreme climatic events (ECEs) such as droughts and heat waves are predicted to increase in intensity and frequency and impact the terrestrial carbon balance. However, we lack direct experimental evidence of how the net carbon uptake of ecosystems is affected by ECEs under future elevated atmospheric CO₂ concentrations (eCO₂). Taking advantage of an advanced controlled environment facility for ecosystem research (Ecotron), we simulated eCO₂ and extreme cooccurring heat and drought events as projected for the 2050s and analyzed their effects on the ecosystem-level carbon and water fluxes in a C3 grassland. Our results indicate that eCO₂ not only slows down the decline of ecosystem carbon uptake during the ECE but also enhances its recovery after the ECE, as mediated by increases of root growth and plant nitrogen uptake induced by the ECE. These findings indicate that, in the predicted near future climate, eCO₂ could mitigate the effects of extreme droughts and heat waves on ecosystem net carbon uptake.

climate change | extreme events | elevated CO₂ | carbon fluxes | grassland ecosystem

Increased aridity and heat waves are projected to increase in the 21st century for most of Africa, southern and central Europe, the Middle East, and parts of the Americas, Australia, and southeast Asia (1–3). These regions have a large fraction of their land covered by grasslands and rangelands, a biome covering approximately one-quarter of the Earth's land area and contributing to the livelihoods of more than 800 million people (4). There is mounting evidence that extreme climatic events (ECEs) may significantly affect the regional and global carbon (C) fluxes (3, 5–9) and potentially feed back on atmospheric CO₂ concentrations and the climate system (7). However, our knowledge concerning the outcome of the interaction between future ECEs and elevated atmospheric CO₂ concentrations (eCO₂) for ecosystem C stocks is equivocal (10–12). Studies focusing on plant physiological responses have shown that eCO₂ has the potential to mitigate future drought-related stress on plant growth by reducing stomatal conductance, thereby increasing water use efficiency (WUE) (13–15) and preserving soil moisture (16–18). However, to date, little is known on whether and how eCO₂ alters the consequences of ECEs for ecosystem net C uptake. Because the capacity of ecosystems to act as a C sink depends on the relative effects of eCO₂, ECE, and their potential interaction on both plant and soil processes, an integrated assessment of all C fluxes during and after the ECEs is important if we are to estimate the overall C balance.

Using the Montpellier CNRS Ecotron facility (www.ecotron.cnrs.fr), we tested with 12 large controlled environment units (macrocosms, *SI Appendix*, Fig. S1) whether (i) an ECE (severe drought and heat wave) predicted for the 2050s reduces ecosystem net C uptake by reducing ecosystem photosynthesis relative to ecosystem respiration (R_{eco}), (ii) eCO₂ buffers the negative effects

of the ECE on ecosystem CO₂ fluxes and increases ecosystem water-use efficiency during the ECE, and (iii) eCO₂ speeds up the recovery of ecosystem C uptake after the ECE. We exposed a seminatural upland grassland (botanical composition see *SI Appendix*, Table S1) from the French Massif Central (45°43'N, 03°01'E, 800 m above sea level) to the average climatic conditions for the 2050s as projected by the downscaled ARPEGEv4 climate model (19). We exposed large (4 m² and 0.6 m depth) and intact ecosystem monoliths in lysimeters to (i) ambient CO₂ (aCO₂ at 390 μmol·mol⁻¹) and predicted elevated levels of atmospheric CO₂ concentrations (eCO₂ at 520 μmol·mol⁻¹) and (ii) the presence/absence of the most severe drought and heat wave (ECE) projected by the above-mentioned climate model over the 2050s. The experiment was based on 12 macrocosm experimental units, using a two factorial crossed design (elevated CO₂ and ECE, each with two levels) with three replicates per treatment combination. The ECE included a reduction in precipitation by 50% during 4 wk in midsummer, followed by 15 d with no precipitation and a concomitant increased temperature by +3.4 °C (Fig. 1). Thereafter, the precipitation was gradually increased during 26 d (see *Methods* for details). In addition to vegetation characteristics, we monitored the net ecosystem CO₂ exchange

Significance

Ecosystems are responding to climate change and increasing atmospheric CO₂ concentrations. Interactions between these factors have rarely been assessed experimentally during and after extreme climate events despite their predicted increase in intensity and frequency and their negative impact on primary productivity and soil carbon stocks. Here, we document how a grassland exposed to a forecasted 2050s climate shows a remarkable recovery of ecosystem carbon uptake after a severe drought and heat wave, this recovery being amplified under elevated CO₂. Over the growing season, elevated CO₂ entirely compensated for the negative impact of extreme heat and drought on net carbon uptake. This study highlights the importance of incorporating all interacting factors in the predictions of climate change impacts.

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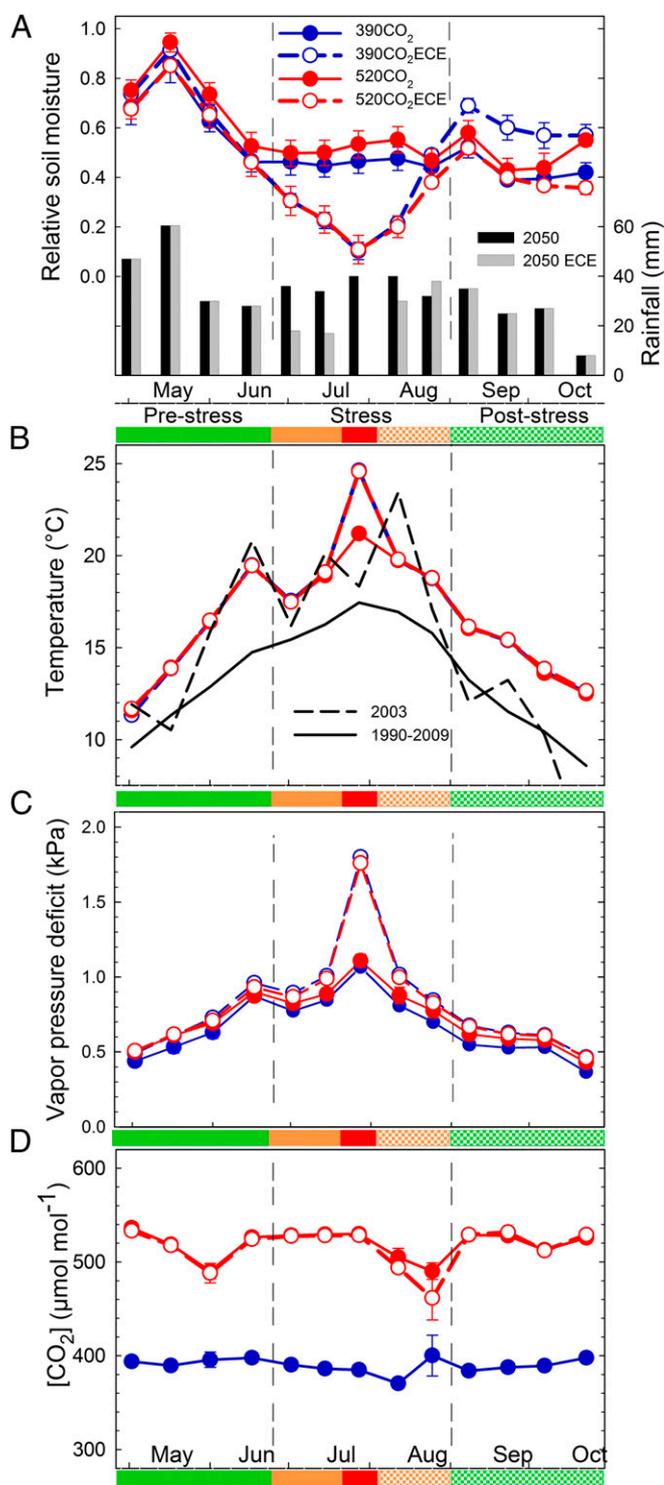


Fig. 1. Ecotron-simulated environmental conditions of the year 2050 under two atmospheric CO₂ concentrations (390 and 520 μmol·mol⁻¹) with and without an ECE. (A) Soil moisture relative to field capacity in the top 60 cm. Bars depict rainfall. (B) Experimentally simulated vs. field recorded temperature (daily means) in the heat wave year 2003 and average of the years 1990–2009 (the simulated temperatures at each CO₂ concentrations are too similar for the blue and red lines to be distinct). (C) Simulated air vapor pressure deficit. (D) Experimentally simulated atmospheric CO₂ concentrations. Data represent means over 14 (±1) d ± SEM of three replicates. Horizontal bars represent the experimental periods (solid green, prestress; solid orange, halved water supply; solid red, no water supply and +3.4 °C temperature increase; hatched orange bar, gradual rewetting; hatched green bar, poststress (see *Methods* for details).

(NEE) and ecosystem evapotranspiration (ET). Furthermore, we derived values of gross primary productivity (GPP), R_{eco}, and WUE for the prestress, stress, and poststress periods.

Results

During the prestress period in spring, ecosystem CO₂ and water vapor fluxes increased with the development of the canopy until the June harvest (Fig. 2). Elevated CO₂ increased GPP (+20%) and WUE (+25%) while slightly decreasing ET (−3%) (Fig. 2 and *SI Appendix*, Table S2). At the June (prestress) harvest, there was no effect of eCO₂ on above-ground biomass. Root growth, however, increased by 77% under elevated CO₂ (marginally significant; *SI Appendix*, Table S3). Canopy greenness, i.e., the fraction of green vs. total above-ground shoot biomass, increased by 41% (*SI Appendix*, Table S3 and Fig. S3B), whereas the shoot nitrogen content (%) and pool (g/m² ground area) decreased under eCO₂ relative to aCO₂ by 9 and 10%, respectively (Fig. 3B and *SI Appendix*, Fig. S4 and Table S4).

When the ECE was imposed (stress period), the mean daily air temperature and vapor pressure deficit peaked at 25 °C and 1.8 kPa, respectively (Fig. 1 B and C). These climatic conditions led to a gradual reduction in soil moisture (Fig. 1A) and canopy greenness (−10%; *SI Appendix*, Table S3 and Fig. S3B). NEE and GPP were significantly affected by the interaction between eCO₂ and ECE, but in a variable manner over time (*SI Appendix*, Table S2). Compared with aCO₂ conditions, the eCO₂ treatment increased GPP and R_{eco} (by +55 and 23%, respectively) during the first month of drought, but this effect disappeared for GPP during the 2 wk with combined drought and heat wave. However, R_{eco} was 35% higher in the eCO₂ + ECE treatment relative to aCO₂ + ECE (Fig. 2C) resulting in a net release of CO₂ from the ecosystem under the eCO₂ + ECE treatment during and immediately after the heat wave (Fig. 2A). During the first month of reduced precipitation, eCO₂ buffered the negative effect of drought on ET and WUE, leading to a higher ET (+6%) and WUE (+51%) under the eCO₂ treatment relative to aCO₂. However, eCO₂ had no lasting impact on ET during and immediately after the heat wave (Fig. 2D and E and *SI Appendix*, Table S2). When precipitation was gradually resumed, in August (Fig. 1A), a progressive recovery of CO₂ and water vapor fluxes was observed in the macrosystems previously exposed to the ECE. The recovery of relative soil water moisture was lower in the eCO₂ + ECE treatment relative to aCO₂ + ECE (Fig. 1A) due to a stronger recovery of ET and other fluxes at elevated CO₂ (Fig. 2D).

During the poststress period (September to November), fluxes of CO₂ and water decreased progressively with decreasing temperature and light levels in both CO₂ treatments without ECE. The eCO₂ treatment significantly increased NEE (+146%), GPP (+46%), R_{eco} (+25%), and WUE (+32%) (Fig. 2 and *SI Appendix*, Table S2). GPP, NEE, and WUE strongly increased in September and reached values significantly higher than in the treatments without ECE (Fig. 2 and *SI Appendix*, Table S2). An eCO₂ × ECE interaction affected the NEE and GPP fluxes, suggesting that the recovery of the CO₂ fluxes led to significantly higher net and gross ecosystem C uptake in the eCO₂ + ECE treatment combination (up to 60% and 240% higher GPP and NEE, respectively in the eCO₂ + ECE treatment compared with the mean of the remaining treatment combinations).

Above-ground biomass at the November harvest did not differ between the treatments (Fig. 3A) and confirmed the low productivity of this grassland type during autumn (20). During the poststress period, compared with aCO₂, eCO₂ increased the Leaf Area Index (LAI) (+47.9%; *SI Appendix*, Fig. S3A) and root growth rate (+244%; Fig. 3C) and decreased the shoot nitrogen

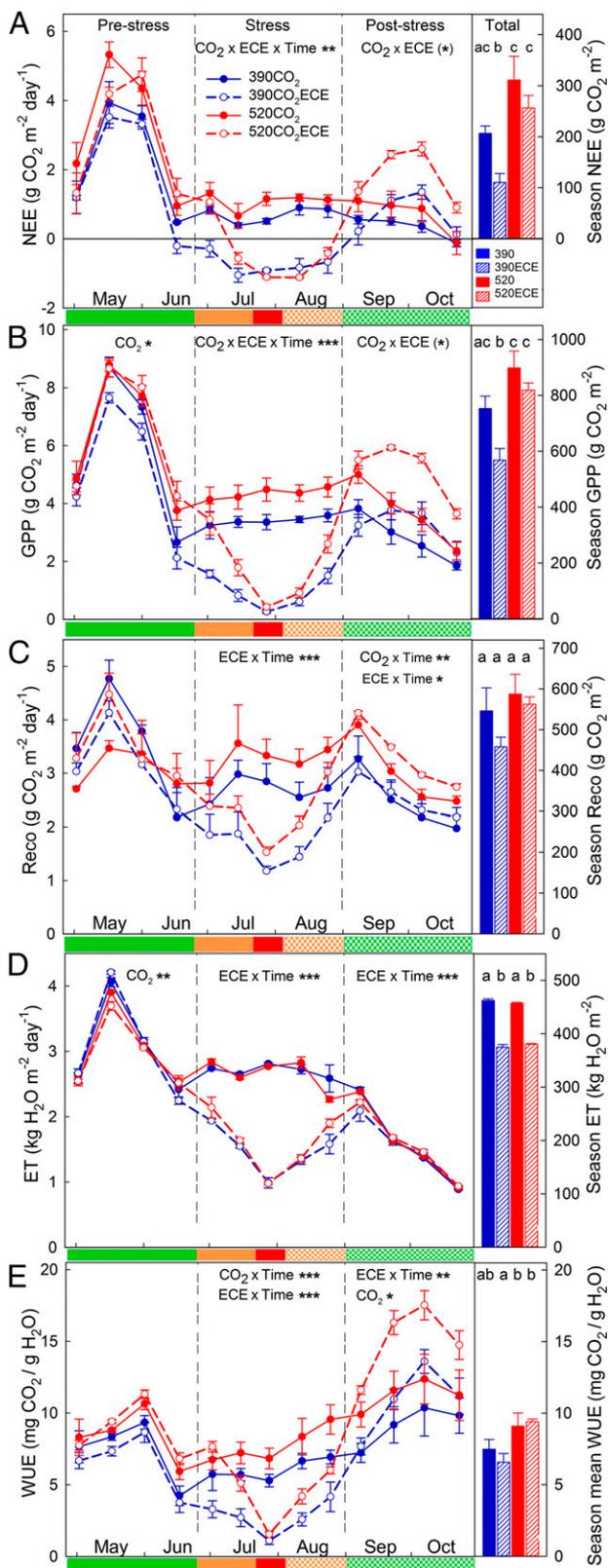


Fig. 2. Seasonal dynamics (Left, lines) and cumulative fluxes (Right, bars) of carbon and water as affected by the CO_2 and ECE treatments. (A) NEE. (B) GPP. (C) R_{eco} . (D) ET. (E) WUE. Data represent means over 14 (± 1) d \pm SEM of three replicates. Stars indicate significant terms according to repeated-measures ANOVAs [*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, and (*) $P < 0.08$]. Different letters above bars denote significant differences between individual means. Horizontal bottom bars represent the experimental periods as in Fig. 1.

content (-21% ; *SI Appendix*, Fig. S4 and Tables S3 and S4). No CO_2 effect was found on canopy greenness or on the shoot nitrogen pool. ECE strongly increased the shoot nitrogen pool ($+87\%$, Fig. 3B) relative to the treatment combinations without ECE (both under $a\text{CO}_2$ and $e\text{CO}_2$), primarily through an increase in the shoot nitrogen content ($+53\%$; *SI Appendix*, Fig. S4 and Table S4). Belowground, the root growth rate and the root nitrogen pool were affected by the $\text{CO}_2 \times \text{ECE} \times \text{Time}$ interaction (Fig. 3 C and D and *SI Appendix*, Fig. S6A and Tables S3 and S4). We also found an $\text{ECE} \times \text{Time}$ interaction on the root nitrogen content, with a significantly higher content in the ECE treatment in September ($+19\%$, $P_{1/10} = 0.029$; *SI Appendix*, Fig. S6B).

These results suggest that the recovery of CO_2 fluxes following the ECE treatments was stimulated by increased nitrogen availability. This suggestion was confirmed by showing that shoot and root nitrogen pools were predictors of late October CO_2 fluxes (GPP and NEE; *SI Appendix*, Table S6). Furthermore, in agreement with this conjecture, we also found that the soil nitrification potential measured after the November biomass harvest was twice as large in the macrocosms that had been exposed to ECE compared with macrocosms not exposed to ECE (Fig. 4A and *SI Appendix*, Table S7).

Integrated over the full growing season (April 26–November 3), $e\text{CO}_2$ significantly increased the cumulative seasonal NEE ($+79\%$), GPP ($+30\%$), and WUE ($+32\%$), whereas the ECE significantly reduced cumulative NEE (-29%), GPP (-16%), and ET (-18%) (bar plot of Fig. 2 and *SI Appendix*, Table S7). Interestingly, whereas effects of $e\text{CO}_2$ and ECE were not additive, the cumulative NEE was 24% higher under the $e\text{CO}_2 + \text{ECE}$ treatment compared with $a\text{CO}_2$ without ECE ($P = 0.027$). This result shows that under the projected climatic conditions of the 2050s, $e\text{CO}_2$ more than compensated the negative impact of extreme drought and heat wave. Under $a\text{CO}_2$, the ECE reduced the ecosystem C balance ($C_{\text{NEE}} - C_{\text{harvested biomass}}$) (Fig. 4B and *SI Appendix*, Table S7), and turned the functioning of the grassland from a small C sink ($19.9 \text{ gC}\cdot\text{m}^{-2}$) to a C source for the atmosphere ($-94 \text{ gC}\cdot\text{m}^{-2}$), a result consistent with the analysis of the consequence of the summer 2003 heat and drought (5, 21). In contrast, under $e\text{CO}_2$, the ecosystem C balance increased and reached $115.0 \text{ gC}\cdot\text{m}^{-2}$ without ECE and remaining a C sink, $46.3 \text{ gC}\cdot\text{m}^{-2}$, with ECE (Fig. 4B).

Most previous studies on the impact of $e\text{CO}_2$ associated with drought and/or elevated temperature did not report whole ecosystem responses, but primarily plant responses at various organizational levels. Generally, they show that $e\text{CO}_2$ alleviates the stress associated with drought and/or elevated temperature (4, 16, 18, 22–28), but some studies found inconsistent responses (29–36). This variability could be linked with the seasonality of precipitation (35, 37) or with the intensity and length of the imposed stress, because the effect of $e\text{CO}_2$ has been shown to be positive under moderate drought and negligible under severe stress when stomata are fully closed (14). Owing to high-frequency measurements of ecosystem-level CO_2 fluxes, we could detect both mitigation effects of $e\text{CO}_2$ on CO_2 fluxes during moderate stress and negative effects of $e\text{CO}_2$ on NEE via an increased R_{eco} during and immediately after the heat wave. Our results show that these apparently conflicting results, which have been previously documented separately, occur at different periods during the growing season and depend indeed on the level of water stress. An increase in R_{eco} under $e\text{CO}_2$ has been shown to be prevalent and to result from improved soil water content and/or enhanced inputs of labile C that prime the decomposition of soil organic matter (38). We show that the negative effect of $e\text{CO}_2$ on NEE via increased R_{eco} is transient and had no substantial impact on the cumulative net C uptake during the growing season. In our experiment, the positive effect of $e\text{CO}_2$ on CO_2 fluxes under moderate stress cannot be explained through a soil water sparing effect as found in some earlier studies (16, 24),

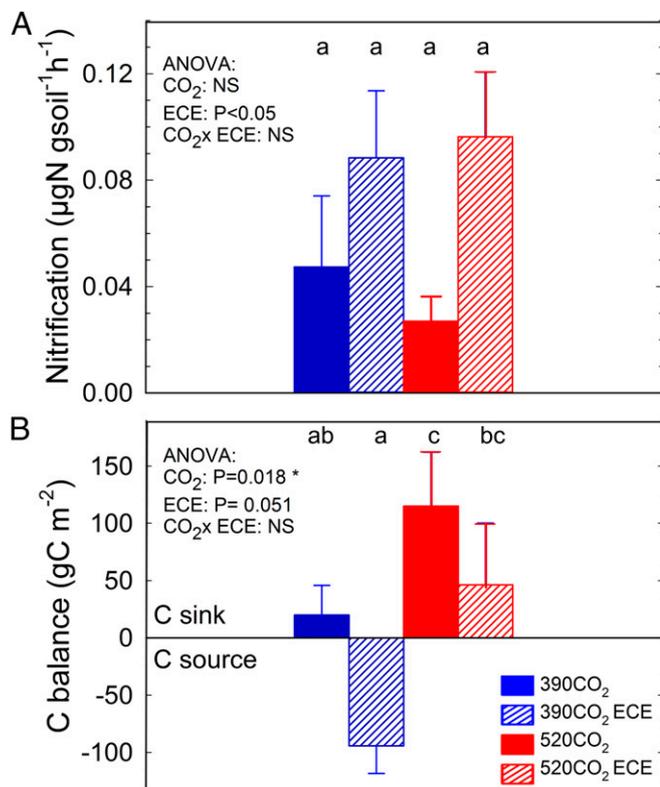


Fig. 4. Soil nitrification potential at the end of the experiment (A) and full growing season (April 26–November 3) ecosystem carbon (C) balance (>0 sink; <0 source) (B) as affected by the CO₂ and ECE treatments. Data are means ± SEM of three replicates. Different letters above bars denote significant differences between individual means.

photosynthetically active radiation transmission of 0.86, a figure matching closely the annual global radiation ratio between Saint-Genès Champanelle and Montpellier during April to September (0.84).

Simulation of ECE. Climate projections for the original location of this grassland for the 2050s (2040–2060) were obtained from the ARPEGEv4 atmosphere-ocean general circulation model with the A2-CO₂ emission scenario (51) and using a multivariate statistical downscaling methodology (19) to generate projections over 8 × 8 km grid. The climatic conditions of an average year of that period were applied from April 2010 to November 2, 2011. From June 25 to August 31, 2011, a summer ECE including combined drought and heat wave (stress period), simulating the severest events projected by the downscaled ARPEGEv4 model, was applied to three randomly selected macrocosms of the six at each CO₂ concentration. For the first four weeks of the stress period (June 25–July 21), the irrigation amount was reduced by half compared with the control. Then, during two weeks (July 22–August 4), irrigation was stopped and the air temperature was increased by 3.4 °C compared with the 2050s average. This increase in air temperature corresponded to 7.1 °C above the 2000–2009 average for the same period, a value above the average of the 14 consecutive hottest days of the exceptional heat wave in summer 2003. From August 5 to 31, irrigation was progressively increased in the treatment with ECE to obtain the same cumulative precipitation in the two treatments during that period.

The Gas Exchange System. Each macrocosm unit of the Montpellier Ecotron is an independent open gas exchange measurement system (52), with a constant flow of air circulating through. The CO₂ flux measurement (NEE) is based on mass balance calculation: The flux of CO₂ exchanged between the ecosystem and atmosphere is calculated from the difference between the fluxes of CO₂ entering and leaving the dome. For this purpose, the CO₂ and water vapor mole fractions are measured at the inlet and outlet (infrared gas analyzers, Licor 7000; Licor), and the mass flow of air at the inlet thermal mass flow meter (Sensiflow iG; ABB). Water vapor mole fraction

measurements are used to correct for the dilution of CO₂ and the variation of airflow rate at the outlet due to the vapor added or removed in the dome by ecosystem transpiration and humidity control. A custom-made manifold system (interconnected solenoid valves, 750 series; Matrix) allows for switching the air fluxes to the infrared gas analyzers from one dome to the other. It takes 12 min to analyze the atmospheric CO₂ concentration of the 12 domes.

Missing values or known inaccurate NEE values during unavoidable experimental work (manual watering, mowing, sampling, checks) caused by the respiration of the persons entering the domes were gap-filled by using the equation $NEE = f(\text{photosynthetically active radiation})$, where f is a rectangular hyperbola fitted with the data of the day before or after the disturbance (53). To provide conservative results, all statistics were performed using only days with less than 33% of gap-filled NEE data. The C flux partitioning algorithm Reichstein et al. (54) (www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php) was used to estimate the daytime R_{eco} .

Other Measurements. Ecosystem evapotranspiration was measured continuously by the lysimeter weight changes over time. Four shear beam load cells with an accuracy of ±200 g (CMI-C3 5,000 kg, Precia-Molen) are used for each lysimeter. WUE was calculated as mg of CO₂ fixed per g of H₂O lost. Soil water content was continuously measured at three soil depths (7, 20, and 50 cm) with TDR probes (TRIME Pico 32, IMKO Micromodul-technik, Germany Ettlingen). Reported data relate to the 0–60 cm depth and are expressed relative to soil water content at field capacity. LAI was estimated with a sunfleck ceptometer (Decagon Devices) from April to October, and canopy greenness was visually estimated every three weeks from June to October. Because extensive management was found to be the best option for sustaining the production of this type of grassland in the context of greater climate variability (20), no fertilization was applied and the number of harvests was low, especially in the summer after the start of the ECE. The vegetation was cut at 5 cm height on March 14, April 26, June 9, and November 3.

Root growth (0–15 cm depth) was measured monthly using four (8 cm diameter) ingrowth cores per macrocosm from February to the end of the experiment. After harvest, shoots and roots were oven-dried (60 °C, 48 h), weighed, and their C and nitrogen content analyzed. Microbial nitrification potential was determined on soil samples collected at the end of the experiment, according to the method of Lensi et al. (55) described in more detail by Pinay et al. (56) (*SI Appendix, SI Methods*).

Statistical Analysis. Linear mixed effects models as available in the R “nlme” package (57) were used to perform repeated-measures ANOVAs on the effects of CO₂, ECE, Time, and their interactions on fortnightly averaged values of carbon and water fluxes, with the Ecotron’s macrocosms as a random factor accounting for temporal pseudoreplication. The statistical models were then simplified to reach the most parsimonious models by using the automatic model simplification “step” procedure based on Akaike’s Information Criterion. Planned pairwise comparisons between the means of the treatments at different time periods were performed by using ANOVAs. As we found a marginally significant interaction between CO₂ and ECE on NEE and GPP during the recovery period, additional time-series analyses on daily values were performed by using mixed effects models with the Ecotron’s macrocosms as a random factor. To account for the temporal autocorrelation of the daily values, these models included autoregressive covariance structure (“correlation=corAR1(form = ~1 | macrocosm”) at the macrocosm level. Following the guidelines of Zuur et al. (58), we found that the models with the day-dependent variance coefficients (“varident(form = ~1 | Day”) fitted best the data and were therefore retained in the models (see *SI Appendix, Table S4* for the complete R syntax).

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