Warming and elevated CO₂ intensify drought and recovery responses of grassland carbon allocation to soil respiration

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Abstract
Photosynthesis and soil respiration represent the two largest fluxes of CO₂ in terrestrial ecosystems and are tightly linked through belowground carbon (C) allocation. Drought has been suggested to impact the allocation of recently assimilated C to soil respiration; however, it is largely unknown how drought effects are altered by a future warmer climate under elevated atmospheric CO₂ (eT_eCO₂). In a multifactor experiment on managed C3 grassland, we studied the individual and interactive effects of drought and eT_eCO₂ (drought, eT_eCO₂, drought × eT_eCO₂) on ecosystem C dynamics. We performed two in situ¹³CO₂ pulse-labeling campaigns to trace the fate of recent C during peak drought and recovery. eT_eCO₂ increased soil respiration and the fraction of recently assimilated C in soil respiration. During drought, plant C uptake was reduced by c. 50% in both ambient and eT_eCO₂ conditions. Soil respiration and the amount and proportion of¹³C respired from soil were reduced (by 32%, 70% and 30%, respectively), the effect being more pronounced under eT_eCO₂ (50%, 84%, 70%). Under drought, the diel coupling of photosynthesis and SR persisted only in the eT_eCO₂ scenario, likely caused by dynamic shifts in the use of freshly assimilated C between storage and respiration. Drought did not affect the fraction of recent C remaining in plant biomass under ambient and eT_eCO₂, but reduced the small fraction remaining in soil under eT_eCO₂. After rewetting, C uptake and the proportion of recent C in soil respiration recovered more rapidly under eT_eCO₂ compared to ambient conditions. Overall, our findings suggest that in a warmer climate under elevated CO₂ drought effects on the fate of recent C will be amplified and the coupling of photosynthesis and soil respiration will be sustained. To predict the future dynamics of terrestrial C cycling, such interactive effects of multiple global change factors should be considered.

Keywords
¹³C labeling, carbon allocation, climate warming, drought, elevated CO₂, gross primary productivity, soil respiration, temperate grassland
1 INTRODUCTION

During the mid- to late 21st century, continued consumption of fossil fuels is expected to increase atmospheric CO₂ concentrations by 300–400 ppm above current levels, leading to global warming of 1–3.7°C and an increase in the frequency and intensity of climate extremes such as drought and heatwaves (IPCC, 2014). These global change factors can cause perturbations of the two largest CO₂ fluxes between terrestrial ecosystems and the atmosphere, that is, gross primary productivity (GPP) and ecosystem respiration (ER), with potential feedbacks to climate change. Of particular importance is the close link between GPP and soil respiration (SR; i.e., the largest component of ER), as plants allocate a significant amount of recently assimilated C to root respiration and rhizo-microbial respiration, often referred to as the autotrophic component of SR (Bahn et al., 2010; Kuzyakov, 2006; Pausch & Kuzyakov, 2018). This link is especially strong and rapid for grassland ecosystems (Bahn et al., 2009; Kuzyakov & Gavrichkova, 2010). However, it is largely unknown whether and how the allocation of recently assimilated C to SR is affected by multiple interacting global change factors such as elevated CO₂ (eCO₂), warming (eT) and drought.

Various experiments and modeling studies suggest that in the future, the combination of eCO₂ and eT can have a complex impact on ecosystem C dynamics. Under eCO₂, plants assimilate more C (Liu et al., 2019; Wang et al., 2012), and allocate more of the photosynthesized C belowground, leading to increases in SR (Figure 1; Adair et al., 2011; Black et al., 2017; Kuzyakov et al., 2019; Song et al., 2019; Wan et al., 2007). Indirectly, eCO₂ also affects SR by preserving soil moisture due to increased plant water use efficiency (Franks et al., 2013; Morgan et al., 2011). On the other hand, warming can increase GPP in cold climates (Wang et al., 2019) and SR (Black et al., 2017) due to accelerated metabolic activity, but can also decrease SR when warming leads to a critical reduction of soil water content (SWC, Figure 1; Fang et al., 2018). Therefore, eCO₂ and eT in combination can either accelerate or reduce C fluxes (Pendall et al., 2013; Wan et al., 2007), depending on the degree to which negative effects of eT on SWC are counterbalanced by positive effects of elevated CO₂ (Figure 1; Blumenthal et al., 2018; Heisler-White et al., 2008; Huxman et al., 2004; Schwinning et al., 2004). Thus, the relative effects of eCO₂ and eT on SWC will also determine whether drought effects on GPP and soil ecosystem respiration are diminished or exacerbated in a future warmer and CO₂-rich environment (Figure 1; Albert et al., 2011; Gray et al., 2016; Obermeier et al., 2017; Roy et al., 2016).

It is well established that GPP and SR are strongly reduced by drought, and that drought effects are more pronounced for GPP than for respiration (Frank et al., 2015; Reichstein et al., 2013; Schwalm et al., 2010). In consequence, the autotrophic component of SR, which relies strongly on C supply from photosynthesis, was shown to be more strongly affected by drought than the heterotrophic component, which derives from the turnover of soil organic matter (Zhou et al., 2016). Isotopic pulse labeling studies suggest that indeed drought reduces the amount of photosynthetically fixed recent C allocated to roots and soil microorganisms (Fuchszieger et al., 2014; Hasibeder et al., 2015; Karlowsky et al., 2018; Sanaullah et al., 2012) and in consequence to SR (Barthel et al., 2011; Blessing et al., 2016; Burri et al., 2014; Hagedorn et al., 2016; Ingrisch et al., 2020; Figure 1). Drought has also been shown to increase the mean residence time of C in the plant–soil system (Chomel et al., 2019; Karlowsky et al., 2018; Ruehr et al., 2009; Zang et al., 2014). However, there is scarce and conflicting evidence to what degree the reduction in the belowground respiratory release of recent C under drought is caused by a reduced supply of recent C (from GPP) or by reduced belowground metabolic C demand. The latter would result in altered belowground partitioning of recently assimilated C and change the fraction of assimilates respired belowground and their residence times (Burri et al., 2014; Ingrisch et al., 2020). While the effects of drought on the coupling of GPP and SR are comparatively well understood under current environmental conditions, there is a major gap in our understanding of how the fate of recent C in the plant–soil system, and in particular soil respiration, during drought and drought recovery is modulated by future conditions, through direct and indirect effects of eCO₂ and eT on SWC and C supply versus demand in belowground respiration (Figure 1).

The overall aim of this study was to understand the effects of drought on grassland C dynamics and the coupling of GPP and SR, and how these drought effects are altered by warming and elevated CO₂. We exposed sections of a managed temperate grassland to

![Conceptual framework and hypothesized effects of elevated CO₂ (eCO₂), warming (eT) and drought on the transfer of recently assimilated carbon (green boxes) to soil respiration. The signs denote the direction of effects. Measured variables are indicated by solid boxes.](image-url)
combined experimental manipulations of temperature, atmospheric CO₂ concentrations and drought, and conducted in situ 13CO₂ pulse labeling campaigns during the peak drought and the recovery periods to trace the allocation of newly assimilated C from plants to soil and to SR. We tested the hypotheses that (1) under ambient conditions drought would reduce ecosystem C uptake, the absolute and relative amount of C allocated to SR and its mean residence time; (2) future conditions with eT and eCO₂ would lead to increased C uptake and SR through increased allocation to belowground fluxes and (3) eT and eCO₂ would reduce drought effects on SWC and the coupling of GPP and SR and thus mitigate the drought impact on the C cycle, and enhance post-drought recovery of SR by increased plant C supply. Furthermore, we expected that (4) the fraction of recent C remaining in the plant-soil system would be increased by drought, more strongly under ambient than under future conditions.

2 | METHODS

2.1 | Study site

The study was conducted as part of the multifactor manipulation experiment “ClimGrass,” which is located at the Agricultural Research and Education Centre, Raumberg-Gumpenstein, Austria (47°29′38″N, 14°06′03″E) at an elevation of 700 m (Piepho et al., 2017). The geographic location and climatic conditions (mean annual temperature: 7.2°C; mean annual precipitation: 1000 mm) are representative of a larger part of montane grasslands in the Alps. The study site is composed of a nutrient-rich, managed mountain grassland on a Cambisol consisting of 44.2% sand, 47.6% silt and 8.3% clay (Deltedesco et al., 2019, 2020). The vegetation is dominated by tall oat grass (Arrhenatherum elatius L.), orchard grass (Dactylis glomerata L.), golden oat grass (Trisetum flavescens L.), meadow fescue (Festuca pratensis L.), bird’s-foot trefoil (Lotus corniculatus L.) and white clover (Trifolium repens L.). The grassland is cut three times during the growing season (end of May, end of July and early October) and fertilized using mineral fertilizer to replace the amount of nutrients removed by the harvests. In 2017, the year of the pulse labeling experiment, the annual precipitation at the site was 1281 mm and the mean air temperature was 8.8°C.

2.2 | Experimental setup and drought simulation

The experiment was performed on eight plots exposed to four treatments: (i) control (i.e., ambient conditions), (ii) drought, (iii) eT and eCO₂ (eT eCO₂) and (iv) eT eCO₂ combined with drought. Air temperature and atmospheric CO₂ concentration were increased by 3°C and 300 ppm above ambient, which corresponds to the climate scenario for the end of the 21st century following to the RCP 8.5 model trajectory (IPCC, 2014). CO₂ enrichment was achieved via a mini free air CO₂ enrichment (FACE) system (Miglietta et al., 1997; Obermeier et al., 2017; Reich et al., 2014), which fumigates the plot during daytime through a circular tube surrounding the plots (Figure S1; Piepho et al., 2017; Pöttsch et al., 2019). Infrared lamps were used to heat the canopy surface temperature 3°C above ambient temperature. Mock frames and fumigation rings and mock IR-lamps were installed in all control plots to ensure that environmental conditions in plots differed only concerning the tested environmental drivers.

In each of the eight plots, 12 stainless steel cylinders of 30 cm diameter and 60 cm height were inserted into the soil during 2014 (Figure S1), which served as intact but physically distinct grassland units (“mesocosms”) precluding any lateral transfer of labeled C. Mesocosms were larger than the ones previously used successfully in a grassland pulse labeling experiment testing for effects of drought on C dynamics (Ingrisch & Bahn, 2018; Ingrisch et al., 2020; Karlowsky et al., 2018). In the study year 2017, we tested for potential plot effects of the mesocosm experiment using aboveground biomass of all 12 mesocosms contained in each plot (n = 4 treatments*2 plots*12 mesocosms = 96). Biomass was sampled during the first annual harvest (cut 1, 2017), which occurred prior to the drought experiment. To test whether “plot” had an effect on mesocosms productivity, we used linear mixed-effect models (R-package lme4 and lmerTest) with “treatment” as fixed effect and “plot” as random effect. The variance of the random effect was very small (2.6) in comparison to the residual variance (148.8) and had only minor effects on the standard errors of means (in comparison to linear model without random effects). Thus, we concluded that plot effects are negligible in this experiment and that the individual mesocosms used in the pulse-labelling study constitute independent units and can therefore be considered “true” replicates. For our study, each of the four treatments (control, drought, eT eCO₂, eT eCO₂ × drought) was replicated with three mesocosms randomly selected from the two plots per treatment. Ecosystem CO₂ fluxes and soil respiration measurements were made on different sets of mesocosms to avoid disturbances through overlapping measurements and samplings.

Soil temperature and volumetric soil water content (SWC) were measured using probes (S-TMB and 10HS, Onset computer corporation) installed in the main rooting horizon 5 cm below the soil surface in two mesocosms located in two different plots per treatment and were recorded (HOBOMicro Station H21-002; Onset computer corporation). The SWC dataset was calibrated using gravimetric soil water content (Figure S2), which was determined by oven drying of fresh soil samples repeatedly collected in all pulse-labelled mesocosms. Air temperature, photosynthetically active radiation (PAR) and relative humidity were continuously measured all around the year by a climate station based at the ClimGrass facility (Figure S3).

The drought treatment was applied using automated rainout shelters, which covered the respective plots during rainfall (Figure S1). The drought treatments started on doy-112 and ended on doy-209 by re-wetting the drought treatment plots with 40 mm of previously collected rainwater for 2 h. Corresponding to the common management of the grassland, the vegetation in all the treatments was cut on doy-208, which was also the last day of the drought treatment. Hence, the post-drought recovery phase concurs with post-cut regrowth phase. Thus, three distinct periods were defined
2.3 | Ecosystem CO₂ flux measurements

Net ecosystem productivity (NEP), ecosystem respiration (ER) and gross primary productivity (GPP) were measured using closed dynamic chambers as described by Ingrisch et al. (2018). Briefly, NEP was measured using a cylindrical transparent plexiglass chamber with a 30 cm diameter and 100 cm height. The chamber was ventilated with fans fitted inside. The chamber had a hole in the top to avoid any pressure effects while placing the chamber, which can be closed. The chambers had sensors inside to measure CO₂ concentration (GMP 343, Vaisala), air temperature and water vapor (HMP 75, Vaisala) for 1 min at 5 s intervals. Mesocosms were always first measured under light conditions to assess NEP, followed by a measurement of ER, for which the chamber was darkened with an opaque cloth. Measurements were quality controlled visually (Pirk et al., 2016) and the CO₂ flux rates were calculated by linear regression, as described by similar studies (e.g., Ingrisch et al., 2018; Schmitt et al., 2010). GPP was calculated as the difference between paired measurements of NEP and ER. To ensure comparability across measurements, we only present light-saturated GPP max and NPP max, defined as fluxes at a photon flux density (PFD) greater than 1400 µmol m⁻² s⁻¹. The measurements were made on three mesocosms per treatment during peak drought (doy-191), and at two time points during recovery (doy-213, 221). The measurements were made in random order of mesocosms on days with clear sky during late morning hours (9:00–13:00 CEST).

2.4 | ¹³CO₂ pulse labeling

Two ¹³CO₂ pulse labeling campaigns were performed, the first during peak drought and the second during the recovery period. For the "peak drought" campaign, 12 mesocosms (three per treatment) were labeled on three consecutive days during doy-197 to 199 (Figure S4). During the recovery campaign, different sets of 12 mesocosms were labeled on each mesocosm. Measurements were quality controlled visually (Pirk et al., 2016) and the CO₂ flux rates were calculated by linear regression, as described by similar studies (e.g., Ingrisch et al., 2018; Schmitt et al., 2010). GPP was calculated as the difference between paired measurements of NEP and ER. To ensure comparability across measurements, we only present light-saturated GPP max and NPP max, defined as fluxes at a photon flux density (PFD) greater than 1400 µmol m⁻² s⁻¹. The measurements were made on three mesocosms per treatment during peak drought (doy-191), and at two time points during recovery (doy-213, 221). The measurements were made in random order of mesocosms on days with clear sky during late morning hours (9:00–13:00 CEST).

The pulse labeling procedure was similar to previous studies (Bahn et al., 2009; Hasibeder et al., 2015; Ingrisch et al., 2020). Pulse labeling was performed on days with clear sky between 09:00 and 15:00 CEST. Transparent plexiglass chambers were placed airtight on each mesocosm. Chambers were ventilated and temperature stabilized using fans and by circulating cold water through tubes inside the chamber. Air temperature, CO₂ concentration (Li-840A, Li-Cor Inc) and ¹³C/¹²C ratio (G2201i Analyzer, Picarro Inc) inside the chamber were continuously monitored and were used to calculate the ¹³CO₂ uptake during labeling. This yielded similar results compared to two alternative approaches to assessing ¹³CO₂ uptake (1) through GPP measured on the plots immediately prior to labeling and (2) through the amount of ¹³C recovered in plant biomass immediately after labeling (Figure S5). Photosynthetically active radiation (PQS1, Kipp & Zonen) was monitored outside the chamber. Before labeling, the CO₂ concentration inside the chamber was reduced to ~200 ppm by plant photosynthesis in the closed chamber and by scrubbing using soda-lime. Labeling started with injecting 15 ml of 99% ¹³CO₂ (Sigma-Aldrich) into the chamber with a syringe. Consecutive pulses of labels were added to maintain 40–70 atom% ¹³C inside the chamber over the complete labeling time of 50–70 min. During labeling, the mean CO₂ concentration in the chamber was 600 ppm ± 200 ppm and mean air temperature was 25°C ± 5°C.

2.5 | Soil respiration and isotopic composition

Soil respiration (SR) and its isotopic composition were measured continuously on the mesocosms that were subjected to labeling. Initially, 12 mesocosms labeled during drought were measured on the last 10 days of drought and 5 days after the rewetting. Afterwards, the soil respiration chambers were moved to the second set of mesocosms that were labeled during the recovery period, where they measured from doy-217 to 228.

A custom made steady-state measurement setup as described by Ingrisch et al. (2020) was used to measure soil respiration and isotope composition (Figure S1). Briefly, it includes 12 cylindrical steady-state flow-through chambers made from white PVC tubes with 4.5 cm diameter. Each chamber had two connections that is, inlet and outlet. The outlet connection had an inner diameter of 4 mm diameter and the inlet tube had a diameter of 3 cm. The inlet of each chamber was connected to a 25 L polyethylene cylinder which acted as buffer volume to stabilize the concentration of CO₂ entering the chamber. The chambers were constantly flushed with air from the buffer volume at a flow rate of 200 ml min⁻¹ to ensure steady-state conditions. The inlet/buffer volume and outlet of all the chambers were connected to an online isotope analyzer (G2201i Analyzer, Picarro Inc) through a custom-made valve multiplexing system. The valve multiplexer switches between the inlet and outlet of each chamber and flushes all chambers continuously with air from the buffer volume to maintain steady-state conditions in the chambers. To assess potential effects of chamber size and setup on soil respiration fluxes, we compared soil respiration data during peak drought with those obtained with using larger (21 cm diameter) automated chambers (Li 8100-104, Li-Cor Inc.) from the same experiment, but on different larger (3 m²) plots (Reinthaler et al, in preparation). We found that the soil respiration data obtained with the custom-made smaller chamber setup used for the present study tended to be higher (on average 14%–25%), but overall covered a similar range as observed with the Licor 8100-104 chambers in the larger plots and yielded comparable treatment effects.

The isotope analyzer measures the concentration of isologues of CO₂ (¹²CO₂ and ¹³CO₂). Each chamber measurement took 12 min: the inlet was measured for 180 s, the outlet was measured
for 360 s and then the inlet was measured again for 180 s. A measurement cycle covering all 12 chambers took 2.4 h. Three calibration gases (400, 1500 and 3000 ppm) with known isotopic composition were measured at the end of each measurement cycle to allow individual span-offset calibration of the analyzer for the two CO₂ isotopologues. The calibration gas with 3000 ppm and δ₁³C of −6.35‰ contained >30 ppm of ¹³CO₂ and exceeded the maximum amount of ¹³CO₂ measured during the chase period, thus allowing us to calibrate the analyzer across the full range of ¹³CO₂ observed in soil respiration (Bowling et al., 2003).

To assess the effect of physical back diffusion of ¹³CO₂ from the soil, two additional mesocosms were pulse-labeled under dark conditions. The same pulse labeling protocol as described above was followed, but the chambers were closed with an opaque cloth to avoid photosynthetic tracer uptake. SR and its isotopic composition were continuously measured for 2 days from labeling. The cumulative amount of ¹³CO₂ efflux from back diffusion ranged from 3.6% to 4.3% of the mean cumulative ¹³CO₂ respired from the soil after labeling under ambient conditions (Figure S6). The correction based on the ¹³CO₂ back diffusion data increased the ¹³CO₂ mean residence times during peak drought by 8.9% and 30.6% in control and drought treatments, respectively, and during recovery by 13.2% and 7.5% in control and drought treatments, respectively (Figure S7). However, the correction for back diffusion did not alter the treatment effects on ¹³CO₂ respiration dynamics and mean residence times. These results were added in the supplementary section.

### 2.6 Sampling of plant and soil material

Aboveground and belowground plant material and soil were sampled before (i.e., natural ¹³C abundance controls, collected immediately next to the mesocosms) and 192 h after each pulse labeling. From each mesocosm, a composite sample of two soil cores with a diameter of 2 and 10 cm depth was taken after sampling plant shoots above this coring area. Soil samples were immediately sieved to 2 mm and fine roots were picked out manually. All samples were immediately frozen and stored in the field using liquid nitrogen. In the laboratory, samples were then freeze-dried for 48 hours, ground and analyzed for bulk δ¹³C and C concentration in each pool using an elemental analyzer (EA 1110: CE Instruments), coupled to a Finnigan MAT Delta Plus isotope ratio mass spectrometer (Thermo Fisher Scientific).

### 2.7 Data analysis and statistics

The SR (in μmol m⁻² s⁻¹) was calculated using time-averaged inlet and outlet CO₂ concentrations, flow rate and the base area of the chamber.

\[
SR = \frac{\text{CO}_2 \text{ (outlet)} - \text{CO}_2 \text{ (inlet)}}{\text{Area of chamber}} \times \text{flow rate}. \tag{1}
\]

The atom fraction of ¹³CO₂ was,

\[
\chi(¹³C) = \frac{¹³\text{CO}_2}{¹³\text{CO}_2 + ¹²\text{CO}_2}. \tag{2}
\]

The ¹³C atom fraction \(\chi(¹³C)\) of SR was calculated as,

\[
\chi(¹³C)_{SR} = \frac{\chi(¹³C)_{\text{outlet}} \times \text{CO}_2 \text{ (outlet)} - \chi(¹³C)_{\text{inlet}} \times \text{CO}_2 \text{ (inlet)}}{\text{CO}_2 \text{ (outlet)} - \text{CO}_2 \text{ (inlet)}}. \tag{3}
\]

The \(\chi(¹³C)_{SR}\) of SR was corrected for \(\chi(¹³C)\) in natural abundance (na) in SR which was derived from pre-labeling measurements to calculate the fraction of ¹³C label in SR

\[
\chi E(¹³C)_{SR} = \chi(¹³C)_{SR} - \chi(¹³C)_{na}. \tag{4}
\]

The absolute amount of ¹³CO₂ (Excess ¹³CO₂ (abs)) respired (in μmol m⁻² s⁻¹) from soil was calculated as,

\[
\text{Excess}^{¹³}\text{CO}_2(\text{abs}) = \chi E(¹³C)_{SR} \times \text{SR}. \tag{5}
\]

The cumulative amounts of soil-respired ¹³CO₂ over a period of 192 h after each pulse labeling were calculated by integrating ¹³CO₂ efflux rates following the trapezoid rule, that is, by linear interpolation between adjacent data points. Therefore, adjacent data points were averaged, multiplied by elapsed time between those data points \((T_i - T_{i-1})\) and summed over the cumulation period.

\[
\text{cum Excess}^{¹³}\text{CO}_2(\text{abs}) = \sum_{i=1}^{n} \left(\frac{\text{Excess}^{¹³}\text{CO}_2(\text{abs})}{2} \right) \times (T_i - T_{i-1}). \tag{6}
\]

The ¹³CO₂ label uptake was calculated using \(\chi(¹³C)\) of CO₂ measured inside the labeling chamber during labeling and GPP measured during pulse labeling (Figure S5). Here, the “T” represents the time elapsed during labeling.

\[
¹³\text{C uptake} = \sum_{i=1}^{n} \frac{\chi(¹³C) \times \text{GPP}}{2} \times (T_i - T_{i-1}). \tag{7}
\]

The amount of label ¹³C recovered in plant biomass (shoot + root) and soil (excess ¹³Cbiomass) was calculated as,

\[
\text{Excess}^{¹³}\text{C}_{\text{biomass}}(\text{abs}) = \left(\chi(¹³C)_{\text{sample}} - \chi(¹³C)_{\text{na}}\right) \times \frac{C_{\text{pool}}}{100}. \tag{8}
\]

Here \(\chi(¹³C)_{\text{na}}\) and \(\chi(¹³C)_{\text{sample}}\) are the ¹³C atom fraction measured in plant and soil samples before and after labeling, respectively. \(C_{\text{pool}}\) represents the amount of C in plants and soil on a per m⁻² soil surface basis, respectively.

The percentage of tracer incorporated into each compartment (plant, soil and respiration) was calculated as,

\[
\text{Excess}^{¹³}\text{C}(\text{relative}) = \frac{\text{Excess}^{¹³}\text{C}(\text{abs})}{¹³\text{CO}_2 \text{ uptake}} \times 100\%. \tag{9}
\]
The coefficient of variation of each chamber-outlet measurement was calculated for CO₂ concentration and \( \delta^{13}C \) as the ratio of standard deviation and mean value. Measurements with a coefficient of variation greater than 0.1 were considered as outliers and removed prior to further analysis. The proportion of flux estimates that were removed based on this filter was 6.2%. A spline function \( (R \text{ function, "smooth.spline," span = 0.5 \text{ day}}) \) was fitted to SR and abs \( ^{13}C \) time series of every mesocosm measurement, to fill data gaps. Then the values were predicted at a 2.4-h interval (representing the measurement interval) based on individual splines to allow grouping between replicates.

An exponential decay function \( (R \text{ function "nls"}) \) was used to calculate the mean residence times of \( ^{13}C \) tracer in SR as the amount of time required to reduce abs \( ^{13}CO_{2} \) respired to 1/e times its initial value (Bahn et al., 2009; Kuzyakov & Gavrichkova, 2010). The abs \( ^{13}CO_{2} \) respiration rates were fitted with an exponential decay model \( y = a + e^{bx} \) \( (R \text{ function "nls"}) \), where \( b \) corresponds to the reciprocal of the mean residence time.

Multiple linear regression analysis was used to analyze the influence of environmental drivers, namely PAR, soil temperature and SWC on soil respiration and on soil-respired \( ^{13}CO_{2} \). To account for the overarching exponential decay in the latter, the residuals of the exponential model were used (hereafter referred to as \( ^{13}CO_{2 \text{ rand}} \)). This transformation focused our analysis on diel patterns by removing variation in the data caused by the exponential decay effect of time (Bahn et al., 2009). This analysis was performed using linear mixed-effect models \( (R \text{ package "nlme"; Pinheiro et al., 2021}) \) with treatment \( (\text{drought/control}) \), the environmental drivers and their interaction as explanatory variables. Replicates were considered as random factors with random intercepts and slopes nested within treatments. The model and regression coefficients were computed for each response variable \( (i.e., \text{soil respired CO}_2 \text{ and } ^{13}CO_{2 \text{ rand}} \text{ within ambient and eT}_eCO_2 \text{ conditions}) \). Temporal autocorrelation in the time series of the response variables was accounted for by using a correlation structure based on a continuous first-order auto-regressive process \( (\text{Brockwell, 2011; corCAR1 in R-package "nlme"; Pinheiro et al., 2021}) \). In addition to the regression coefficients \( (\text{beta}) \), standardized regression coefficients were calculated to compare the relative effects of the explanatory variables. The standardized regression coefficients of each explanatory variable were calculated as the product of its regression coefficient and the ratio of standard deviations of the explanatory variable and the response variable \( (\text{Lorah, 2018; Snijders & Bosker, 2012}) \). The significance of the regression coefficient and the interaction effect \( (\text{driver*drought}) \) was inferred from the \( p \) value \( (<0.05) \) of the regression coefficient.

We explored the temporal lags between environmental drivers and soil CO₂ and \( ^{13}CO_{2 \text{ rand}} \) fluxes by stepwise shifts in the time series of response variables followed by repeating the model computation described above. Time series were shifted by time intervals of 2.4 h \( (\text{which correspond to the measurement intervals for CO}_2 \text{ fluxes as detailed above}) \) spanning a range between -12 and +12 h. Shifting the time series of the environmental drivers and soil respiration to each other alters the regression coefficients of the predictors and allows to identify most probable lags between the fluxes and their drivers. The time lag, at which the maximum regression coefficient of the environmental driver and the flux was observed, indicates the most probable time lag. Negative values of the time lag indicate that the environmental driver leads before response variable and that, therefore, the flux lags after the environmental driver. To examine the time delay in the heat transfer from sunlight to different soil depths, the lag of soil temperature at two soil depths \( (3 \text{ and } 5 \text{ cm}) \) to PAR was also tested using cross-correlation analysis \( (\text{see Figure S8}) \).

The effects of drought, e\( T_eCO_2 \) and their interaction on CO₂ fluxes \( (\text{GPP, ER, NEP and SR}) \) and excess \( ^{13}C \) \( (\text{absolute and relative}) \) in plant, soil and soil respiration were tested for each measurement campaign separately using permutation ANOVA \( (\text{R-package "ImPerm"; Wheeler & Torchiano, 2016}) \). All data processing and statistical analysis were done in R \( (\text{Version 3.4.1; R Development Core Team (2008–2010)}) \).

### RESULTS

#### 3.1 Ecosystem CO₂ fluxes

Under warming combined with elevated CO₂ \( (eT_eCO_2) \), soil water content \( (\text{SWC}) \) was reduced on average by 14% compared to ambient conditions \( (\text{Figure S2c,d}) \). Drought reduced SWC to less than 15% \( (\text{vol under both ambient and eT}_eCO_2 \text{ conditions}) \). The simulated rain event ending the drought treatments did not fully restore SWC and only after a natural rain event a week after the rewetting, SWC in drought-treated plots recovered to values observed in the control treatment.

\( eT_eCO_2 \) did not significantly affect CO₂ fluxes on the ecosystem scale \( (\text{Figure 2, Table S1}) \). During peak drought \( (\text{doy-192}) \), \( \text{GPP}_\text{max} \) was reduced by 48–50% and \( \text{ER} \) was reduced by 28% relative to the controls, irrespective of ambient or e\( T_eCO_2 \) conditions \( (\text{Table S1}) \). Phytomass in all mesocosms was harvested the day before the rewetting, which strongly reduced \( \text{GPP}_\text{max} \). After rewetting, drought had negative legacy effects on the recovery of \( \text{GPP}_\text{max} \) from harvest under ambient, but not under e\( T_eCO_2 \) conditions, where recovery was generally faster than under ambient conditions. ER was not affected by cutting, but increased with progressing recovery under e\( T_eCO_2 \).

#### 3.2 \( ^{13}C \) tracer in plant, soil and soil respiration

Drought reduced the amount of excess \( ^{13}C \) remaining in plants 8 days after pulse labeling under both ambient and e\( T_eCO_2 \) \( (\text{Figure 3a; Table S2}) \). The amount of excess \( ^{13}C \) recovered in soil was generally small and was not significantly affected by drought under ambient conditions, but was reduced to below detection limit under e\( T_eCO_2 \) \( (\text{Figure 3b}) \). Under drought, the total amount
of $^{13}$C respired belowground was strongly reduced, the effect being stronger under eT$_{eCO_2}$ than under ambient conditions (Figure 3c). Drought did not affect the proportion of $^{13}$C label (relative to the total amount taken up) in plant biomass (Figure 3d; Table S2), but it reduced the proportion of $^{13}$C respired in soil and remaining in soil under eT$_{eCO_2}$ (Figure 3e,f).
During recovery from drought, the absolute amount and proportion of $^{13}$C in plant biomass and in soil respiration remained largely reduced under ambient conditions, but less so under eT_eCO$_2$ (Figure 3g–l). Across all treatments, during the recovery period, a distinctly larger amount of $^{13}$C remained in the soil compared to the drought period, amounting to up to 108 mg $^{13}$C m$^{-2}$ and up to 16% of the $^{13}$C label taken up by the plants.

### 4.1 Carbon dynamics and drought responses of recently assimilated C in soil respiration under ambient conditions

Our time-series analysis indicates that the diel variation of SR was directly related to PAR, which was followed by SR by c. 2 h (Figure 5). Radiation can affect respiration by increasing photosynthesis and thereby C supply to the autotrophic component of respiration (roots and the associated rhizosphere microbiome), or by warming the soil and therefore enhancing metabolic rates (Kuyzakov & Gavrichova, 2010). Our analysis indicates that temperature was not the primary driver for SR dynamics, because even in the uppermost soil layer (3 cm) temperature lagged behind PAR and respiration by several hours (Figure 5; Figure S8). This suggests that diel SR dynamics were primarily driven by photosynthesis, and thus by the autotrophic rather than the heterotrophic component of respiration (Vargas et al., 2011; Zhang et al., 2018), the coupling of photosynthesis and SR in response to interacting global change drivers is so far poorly understood. Here, we combined time-series analysis and in situ isotopic pulse labeling to assess the effects of drought and drought recovery under ambient versus future conditions of warming combined with elevated CO$_2$ on ecosystem C dynamics and the linkage between plant C uptake and SR. We found that the combined effects of warming and eCO$_2$ increased SR and the proportion of recently assimilated C respired in soil. At the same time, it altered the drought- and post-drought responses of ecosystem CO$_2$ fluxes and the partitioning of recently assimilated C between plants, soil and SR, highlighting significant interactive effects between the three global change factors.

### 4. DISCUSSION

While it is well established that photosynthesis can play a major role in driving SR and its dynamics (Kuyzakov & Gavrichova, 2010; Vargas et al., 2011; Zhang et al., 2018), the coupling of photosynthesis and SR in response to interacting global change drivers is so far poorly understood. Here, we combined time-series analysis and in situ isotopic pulse labeling to assess the effects of drought and drought recovery under ambient versus future conditions of warming combined with elevated CO$_2$ on ecosystem C dynamics and the linkage between plant C uptake and SR. We found that the combined effects of warming and eCO$_2$ increased SR and the proportion of recently assimilated C respired in soil. At the same time, it altered the drought- and post-drought responses of ecosystem CO$_2$ fluxes and the partitioning of recently assimilated C between plants, soil and SR, highlighting significant interactive effects between the three global change factors.

### 3.3 Dynamics of soil respiration and respired $^{13}$C in relation to environmental drivers

In the absence of drought, eT_eCO$_2$ enhanced diel dynamics and doubled SR (Figure 4b and Figure S9; Table S1). Under drought, cumulative SR was significantly decreased under both ambient and eT_eCO$_2$ conditions (Figure 4c; Table S1). The drought effect was larger under eT_eCO$_2$ (−50%) compared to the ambient conditions (−32%) (Figure 4c). During the recovery period, 3 weeks after the end of the drought, there were no significant effects of drought or eT_eCO$_2$ on the cumulative amount of SR (Table S1; Figure 4m).

The $^{13}$CO$_2$ tracer was recovered in soil respiration immediately after the pulse labeling had ended, reflecting a rapid allocation of photosynthetically fixed C to SR (Figure 4d,e). Tracer efflux rates declined exponentially over time (Figure 4d,e). The decay rates derived from the exponential models indicate that drought under eT_eCO$_2$ conditions increased the mean residence time (Figure 4f) of recent carbon respired from soil. During the recovery period, the mean residence time of soil respired $^{13}$CO$_2$ was decreased in all the treatments compared to the peak drought period (Figure 4p). Drought effects on the mean residence time (Figure 4p) prevailed under ambient but not under eT_eCO$_2$ conditions.

We tested for potential effects of environmental drivers, including soil temperature, soil water content (SWC) and photosynthetically active radiation (PAR) on the diel dynamics of soil respired CO$_2$ and $^{13}$CO$_2$ (i.e., the residuals from the background decay trend, $^{13}$CO$_2$$_{rd}$) using time-series-regression analysis (Figure 5; SWC is not displayed as it did not show any distinct diel variation; Tables S3 and S4). Under ambient conditions soil respired CO$_2$ and $^{13}$CO$_2$$_{rd}$ lagged after PAR by 2.4 h (Figure 5a,b; Tables S3 and S4). By contrast, soil temperature lagged after soil respired CO$_2$ and $^{13}$CO$_2$$_{rd}$ (Figure 5a,b; Tables S3 and S4). Drought dampened the diel dynamics of soil respired CO$_2$ and $^{13}$CO$_2$$_{rd}$ (Figure 4a,d) and increased the time lags of soil respired CO$_2$ following PAR (Figure 5a,b; Tables S3 and S4).

Under eT_eCO$_2$, the diel variation of soil respired CO$_2$ and $^{13}$CO$_2$$_{rd}$ was higher (Figure 5a,b) and the lag of $^{13}$CO$_2$$_{rd}$ after PAR was shorter compared to ambient conditions (Figure 5; Tables S3 and S4). Under eT_eCO$_2$, drought did not affect the diel dynamics of soil respired CO$_2$ and $^{13}$CO$_2$$_{rd}$ (Figure 4) but increased the explanatory power of PAR on soil respired CO$_2$ when soil respired CO$_2$ was lagged after PAR by 2.4 h (Figure 5a,b; Table S3). Under eT_eCO$_2$, soil temperature was generally lagged after $^{13}$CO$_2$$_{rd}$ (Figure 5b).
to SR (Figure 4c,f; hypothesis 1), which is consistent with findings from earlier C allocation studies (Barthel et al., 2011; Hagedorn et al., 2016; Ingrisch et al., 2020; Ruehr et al., 2009). Our understanding of drought effects on the partitioning of recent C to SR is still controversial: previous studies found that the proportional allocation of C to soil and root respiration grasslands may be increased or reduced under drought (Burri et al., 2014; Hasibeder et al., 2020; Ruehr et al., 2009). In our study, the relative amount of
C respired in soil was reduced by drought (Figure 3f), which could reflect changes in source–sink relationships and in C demand for osmolytes and storage versus catabolic C demand (Hasibeder et al., 2015), as discussed in more detail in the subsequent section.

4.2 Carbon dynamics and drought responses of recently assimilated C in soil respiration under warming and elevated CO₂

The warming and elevated CO₂ scenario tested in our study corresponds to a likely scenario projected for the Alpine region in the coming decades (+300 ppm CO₂, +3°C; Gobiet et al., 2014; IPCC, 2014). While the combination of eT and eCO₂ had no clear effects on GPP (Figure 2a), it resulted in a significant increase in SR compared to ambient conditions (Figure 4b,c; Table S1). This was expected because eCO₂ increases belowground C input and turnover (Kuzyakov et al., 2019; van Groenigen et al., 2017; Yue et al., 2017; Zhou et al., 2016), which is also reflected by a higher absolute amount of recent C respired (Figure 3c) and a reduced lag of ¹³CO₂ efflux to PAR (Figure 5b); furthermore, under non-moisture limiting conditions, eT increases microbial activity and respiration (DeAngelis et al., 2019; Melillo et al., 2002; Yanni et al., 2020; but see Alvarez et al., 2018; Figure 1). Correspondingly, the proportion of recent C (relative to uptake) in SR increased (Figure 3f; Table S2; hypothesis 2), which suggests that in a future environment the increased source strength caused by eCO₂ overrides possible effects of eT on increased C demand for belowground metabolism (sink strength).

The future eT_eCO₂ scenario also led to a decrease in SWC in control plots, but less so under drought conditions, where SWC was similar under both ambient and eT_eCO₂ conditions (Figure S2). This indicates that the negative effect of eT on SWC was more pronounced than the water-saving effect of eCO₂ under non-drought conditions (see also Morgan et al., 2011), but that the antagonistic effects of eT and eCO₂ cancelled each other out during drought. Interestingly, drought effects on SR and on the amount and the proportion of recent C allocated to SR were nevertheless more severe under eT_eCO₂ compared to the ambient conditions (Figure 3c,f; Table S2). However, strikingly, under drought the diel dynamics of SR persisted under eT_eCO₂ (Figure 4b), and diel peaks remained strongly related to PAR (Figure 5a), suggesting that the enhancing effect of eCO₂ on autotrophic respiration persisted also during conditions of severe drought. This apparent discrepancy between the reduced use of ¹³C in SR and the sustained coupling of photosynthesis and SR in drought under eT_eCO₂ can be reconciled if one considers that the allocation of recent C could have shifted dynamically between storage and respiration as drought progressed: at the point of pulse labeling a significant portion of recent C could have been preferentially allocated to starch and/or osmotically active fructans and sugars (Barthel et al., 2011; Hasibeder et al., 2015; Karlowsky et al., 2018), reducing the fraction of ¹³C in SR. When demand for these compounds was satisfied as drought progressed, an increasing portion of subsequently photosynthesized C might again have been preferentially used for immediate catabolic processes, indicated by the sustained coupling of PAR and SR during peak drought. This hypothesized dynamic response of the use of freshly assimilated C for belowground
processes under drought is consistent with our finding concerning the mean residence time of $^{13}$C (Figure 4f), whose increase under eT$_e$CO$_2$ conditions indicates a reduced $^{13}$C turnover, possibly caused by initial preferential storage and subsequent slow release of small amounts of $^{13}$C for fuelling respiration.

### 4.3 Recovery responses and ecosystem implications

When assessing the overall resilience of ecosystem processes to drought, it is essential to also evaluate post-drought recovery effects (Ingrisch & Bahn, 2018), given their importance for the ecosystem C budget (Frank et al., 2015). We found that eT$_e$CO$_2$ enhanced the recovery of GPP compared to the ambient conditions (Figure 2d; hypothesis 3), which supports the finding from an earlier experimental study (Roy et al., 2016) and a larger-scale assessment (Schwalm et al., 2017). Drought effects on SR recovered under both ambient and eT$_e$CO$_2$ conditions (Figure 4k–m and S9), but eT$_e$CO$_2$ accelerated the recovery of the amount and the speed of recently assimilated C respired from soil (Figures 3i–l and 4p; hypothesis 3). These results suggest that while eT$_e$CO$_2$ can increase the severity of drought effects on grassland C dynamics, it can also increase recovery rates and the amount of recent C allocated to belowground metabolic processes.

From an ecosystem C budget perspective, it is essential to quantify not only the fraction of assimilated C, which is returned to the atmosphere by soil respiration, but also the fraction and the amount remaining in the plant–soil system (Hartmann et al., 2020; Jiang et al., 2020). Our pulse-labeling study showed that by the end of the respective chase periods only a small portion (1%–16%) of recently assimilated C was recovered in the soil, while 16%–45% was retained in the plant biomass, both the fractions and the amount being larger during the recovery period (Figure 3g–l). Drought caused significant reductions in the amount of recent C in all components (Figure 3a–c), but, interestingly, had no clear effect on the fraction of tracer allocated to plant biomass both under ambient and eT$_e$CO$_2$ conditions. The strong drought-induced reduction in the partitioning of recent C to the plant, soil and SR combined, especially under eT$_e$CO$_2$ (Figure 3d–f), implies that the fraction of recent C respired aboveground was strongly increased. This shift of the use of recent C from below- to aboveground respiration under drought was unexpected. It could have been caused by increased water stress-induced metabolic demand, which has been suggested to be species-specific and related to stress intensity (Dahal & Valnerbergh, 2017; Rowland et al., 2021; Varone & Grattani, 2015), but has not yet been studied for grassland species. Interestingly, during recovery from drought a distinct drought legacy could be observed under ambient conditions, leading to a reduced allocation of recent C to plant biomass and SR, while no significant reductions were found under eT$_e$CO$_2$. This highlights the potential for a more rapid drought recovery of C dynamics under future warmer conditions in a CO$_2$-rich world (Roy et al., 2016). While we recognize that for obtaining a longer-term perspective of global change effects on the ecosystem C balance the stabilization and decomposition of plant- and microbial-derived C in soil organic matter need to be considered (e.g., Lavalee et al., 2020; Liang et al., 2017; van Groenigen et al., 2017), our findings highlight large shifts in C allocation and partitioning under climate change, which could represent an important mechanism underpinning also potential long-term effects.

### 5 CONCLUSION

In conclusion, compared to ambient conditions, the combination of eT and eCO$_2$ (1) increased the fraction and the absolute amount of freshly assimilated C in soil respiration, (2) increased the severity of drought effects on the fate of recent C in soil respiration and amplified dynamic shifts between storage and respiration, which led to sustained coupling between photosynthesis and autotrophic soil respiration, and (3) favored the recovery of gross primary productivity, plant regrowth and the amount and the proportion of recent C respired belowground. Our findings therefore indicate that a warmer climate under eCO$_2$ can alter drought and post-drought responses of ecosystem CO$_2$ fluxes and of C allocation from photosynthesis to belowground respiration. This highlights the importance of accounting for the interactions of multiple global change factors to understand and predict future dynamics of the terrestrial C cycle.

### ACKNOWLEDGEMENTS

This study was financially supported by Austrian Science Fund (FWF; P28572-B22). KM was additionally supported by a PhD completion grant from the University of Innsbruck. We thank the team from the Agricultural Research and Education Centre (AREC) Gumpenstein for their support at the ClimGrass-facility. We also thank Mario Deutschmann and Herbert Wachter for their technical support, Lisa Geres for assistance with the fieldwork, Hans-Peter Piepho for statistical advice and Markus Reichstein for advice concerning the time-series analysis.

### CONFLICT OF INTEREST

The authors declare no conflicts of interest.

### AUTHORS’ CONTRIBUTIONS

MB conceived and supervised the study; KM, JI, DR and LM performed the field measurements; AC, AR and WW collected the plant and soil material and measured their C isotope content; KM and JI analyzed the data; EMP and DR maintained the experimental infrastructure; KM and MB wrote the paper with significant inputs from JI, and all co-authors provided feedbacks and comments on the manuscript.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo repository at https://doi.org/10.5281/zenodo.4643297.
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