CLIMATE FEEDBACKS

Drought-induced peatland carbon loss exacerbated by elevated CO_2 and warming

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Extreme drought events are predicted to increase with climate change, yet their impacts on ecosystem carbon dynamics under warming and elevated carbon dioxide (eCO_2) remain unclear. In a peatland experiment with five warming treatments each under ambient carbon dioxide (aCO_2) and eCO_2 (+500 parts per million), a 2-month extreme drought in 2021 reduced net ecosystem productivity by 444.0 ± 65.8 and 736.6 ± 57.8 grams of carbon per square meter at +9°C under aCO_2 and eCO_2, respectively—228.6 ± 56.8% and 381.9 ± 83.4% of the reduction at +0°C under aCO_2. This exacerbation was driven by warming-induced water table decline, prolonged low water tables, and CO_2-enhanced substrate availability through increased plant carbon inputs. Findings indicate that future climate will greatly amplify carbon loss during extreme drought, reinforcing positive carbon-climate feedbacks.

The latest Intergovernmental Panel on Climate Change (IPCC) report projects extreme drought events to become 1.7 to 7.2 times more frequent if the surface temperature increases by 4°C in the near future (*1*). Studies examining the effects of extreme drought under current climates (*2*–*7*) suggest that more frequent extreme drought events have the potential to substantially affect ecosystem carbon (C) cycling. For example, Ciais *et al.* reported a 30% decline in gross primary productivity over Europe during the 2003 European summer drought, resulting in a net C release of 0.5 Pg C $year^{-1}$, which is equivalent to 4 years of C sequestration under nondrought conditions (*8*). Similarly, Wolf *et al.* found that the 2012 US summer drought reduced net ecosystem productivity (NEP) by 0.23 Pg C per season throughout the United States, with a 71% reduction in the Great Plains, United States (*9*). These severe impacts represent large-scale declines in plant growth and increased mortality (*4*, *5*), which can offset ecosystem C sinks and even reverse them into C sources across both time and space (*3*, *5*, *10*–*13*). Such disruptions could intensify positive climate-C feedback, accelerating future warming (*14*, *15*). However, how extreme drought events will influence NEP in a future world with higher temperatures and elevated carbon dioxide (eCO_2) concentration remains unclear.

Field experiments offer opportunities to study the impacts of extreme drought events on ecosystem C processes under future climate scenarios (*16*, *17*). For example, during experimental warming that increased soil temperature by up to 2.6°C and air temperature by 1.1°C in a tallgrass prairie of the Great Plains from 1999 to 2019, an extreme drought event in 2011 reduced NEP by 23.5% under ambient temperature but 53.5% under warming with clipping (*18*). In a temperate peatland ecosystem, an extreme summer drought event in 2018 reduced NEP by approximately 57.8% compared with a nondrought year (2020) under ambient temperature and by around 146.2% under +3.2°C warming (*19*). In addition to warming, eCO_2 is another key driver of future climates. Numerous studies in upland ecosystems have shown that eCO_2 can mitigate the negative drought impacts on ecosystem C sequestration by stimulating photosynthesis (*20*–*22*), conserving water (*21*, *23*, *24*), and improving plant water-use efficiency (*22*, *25*). However, to the best of our knowledge, no studies have examined the impacts of naturally occurring extreme drought events on NEP in a field experiment combining eCO_2 and warming in peatland or other ecosystems (*26*).

Peatlands, although covering only 3% of the land surface, store around 500 billion tonnes (Gt) C (nearly one-third of the world's soil C or about half of the C stored in the atmosphere) because of waterlogging conditions that inhibit decomposition (*27*–*29*). Climate warming driven by eCO_2 and associated extreme events pose a great threat to peatland C sequestration (*30*–*32*). Understanding how the large peatland C stocks respond to extreme drought events under combined warming and eCO_2 is essential so that we can accurately predict the global C budget and future climate. To study peatland response to future climate scenarios, the Spruce and Peatland Responses Under Changing Environments (SPRUCE) project was established as a long-term field experiment that has five whole-ecosystem warming levels (+0°, +2.25°, +4.5°, +6.75°, and +9°C) each under two CO_2 levels (ambient and +500 parts per million) in a northern boreal peatland in Minnesota, United States. The warming gradients were designed to capture the upper limit (8.3° ± 1.9°C) of projected high-latitude warming under Representative Concentration Pathway 8.5 (RCP8.5) by 2100 (*33*).

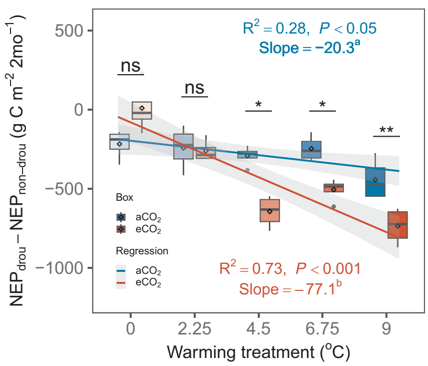

Fig. 1. Effects of extreme drought on NEP under different warming and CO_2 scenarios. NEP_{drou} and $NEP_{non\text{-}drou}$ represent NEP in the 2 months (July and August) in drought year 2021 and nondrought years, respectively. The lower and upper boundaries of the boxplots indicate the 25th and 75th quartiles. The center lines indicate the median values, the rhombus-shaped points inside the boxes indicate the mean values, and the whiskers indicate 1.5 times the interquartile range (IQR). The fitted lines indicate regressions, and the shaded bands indicate 95% confidence intervals (CIs). Different letters denote significantly different slopes. *P* values were adjusted by using the Benjamini-Hochberg false discovery rate correction for multiple comparisons. Differences between aCO_2 and eCO_2 under each warming treatment are ns, not significant; **P* < 0.05; ***P* < 0.01.

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An extreme drought event at the SPRUCE site in 2021 (July–August) substantially lowered the water table to levels below the 10th percentile of the historical range from 1961 to 2021 (fig. S1). The average water table during this period was 411.93 m above sea level, close to the lowest record of 411.82 m during the same period in 1976, the driest year since 1961. This drought lowered the water table depth (WT) by 0.24 m on average in the control plot [+0°C under ambient CO_2 (aCO_2)], which is consistent with reported declines of 0.2 to 0.3 m in other northern peatlands during extreme drought events (*34*–*36*). Taking advantage of this concurrence of a peatland warming and eCO_2 experiment with an extreme drought event in 2021, we explored the response of peatland NEP to the natural extreme drought event under five warming and two CO_2 levels. We hypothesize that (i) an extreme drought event and warming promote reduction in NEP, likely by exacerbating water table drawdown, increasing soil aeration, and enhancing microbial decomposition, and (ii) eCO_2 offsets the NEP reduction, potentially buffering the C loss under extreme drought and warming.

Effects of extreme drought on NEP under warming and eCO_2

The extreme 2-month drought (July and August) in 2021 significantly reduced NEP by 217.9 ± 46.4 g C m^{-2} (mean ± SE) ($P < 0.05$) at ambient temperature and aCO_2 in comparison with that in nondrought years (2016–2019) (no measurement was made in 2020 because of the COVID-19 pandemic) (Fig. 1). This drought effect is comparable in magnitude with the annual NEP declines (range, 218 to 234 g C m^{-2}) reported in other northern peatlands because most of these annual losses occurred during the drought period (*37*, *38*). At ambient temperature and eCO_2, the NEP insignificantly increased by 8.6 ± 79.4 g C m^{-2} ($P > 0.05$) (Fig. 1) during the drought event, likely because of enhanced water-use efficiency and photosynthesis under eCO_2 offsetting the negative impact of drought (*22*, *25*, *26*, *39*). However, at +9°C, the drought event caused a notable decrease in NEP by 444.0 ± 65.8 g C m^{-2} ($P < 0.01$) under aCO_2 and 736.6 ± 57.8 g C m^{-2} ($P < 0.01$) under eCO_2 over 2 months compared with NEP in the nondrought years (Fig. 1). The NEP response to the extreme drought under warming and eCO_2 was primarily due to increased ecosystem respiration (ER). Both of the factors (warming and eCO_2) significantly amplified the drought-induced increase in ER (fig. S2, A and B). Specifically, ER increased by 513.7 ± 44.0 g C m^{-2} ($P < 0.01$) under aCO_2 and 651.7 ± 98.1 g C m^{-2} ($P < 0.01$) under eCO_2 at +9°C during this extreme drought compared with that in the nondrought years.

Mechanisms driving amplified C loss under eCO_2 during drought

The difference in drought effects on NEP between aCO_2 and eCO_2 was significantly negatively correlated with drought-induced changes in number of days with WT below −0.25 m (Fig. 2 and table S1). As shown in fig. S3, significant correlations emerged only when the water table fell below −0.25 m, suggesting it as a critical threshold for strong C flux response to drought. This aligns with the range of −0.2 to −0.3 m that is reported for other peatlands where C cycling is strongly affected (*40*–*43*). In addition, drought-induced declines in WT and increases in vapor pressure deficit (VPD) led to greater increases in ER under eCO_2 (fig. S4 and table S2). eCO_2 could amplify the increase in ER induced by water table decline by enhancing the supply of labile C from leaf litterfall and root exudation (*44*–*46*), which facilitate decomposition, and by accelerating belowground C turnover (*47*, *48*). Globally, eCO_2 significantly increases leaf and root biomass by 21 and 45%, respectively; increases microbial biomass by 21%; and stimulates soil respiration by nearly 30% (*47*). At the SPRUCE site, we also found increased plant-derived C substrates under eCO_2. Before the eCO_2 treatment started in 2014, peat soil carbohydrate concentrations were similar between plots assigned to aCO_2 and eCO_2 treatments. However, they increased significantly in the eCO_2 plots after 4 years of eCO_2 treatment in 2019 ($P < 0.01$) (Fig. 3), averaging 33.7% compared with 28.7% under aCO_2 across the soil profile to a depth of 2 m. Moreover, hydrolysable biopolymers increased by nearly 20% under eCO_2 after 2 years of the eCO_2 treatment (*49*), which may contribute to the overall 5% increase in carbohydrate content and higher porewater CO_2 concentrations under eCO_2 across the peat soil profile, at depths of up to 2 m (Fig. 3) (*50*). Thus, as drought deepened the water table, more C substrates accumulated under eCO_2 became exposed to oxygen, leading to increased CO_2 release through respiration.

As the number of days with WT below −0.25 m increased, the effect of eCO_2 on the impact of drought on gross ecosystem productivity changed from mitigation to exacerbation (fig. S5 and table S3), reflecting a dependence on drought duration, which in our study was mainly driven by the warming treatments. Under a short-term drought condition, eCO_2 generally enhances photosynthesis and water-use efficiency while delaying stomatal closure, allowing plants to maintain higher C uptake (amplified CO_2 fertilizer effect) (*25*, *39*, *51*). However, prolonged severe drought can impair stomatal function and photosynthetic

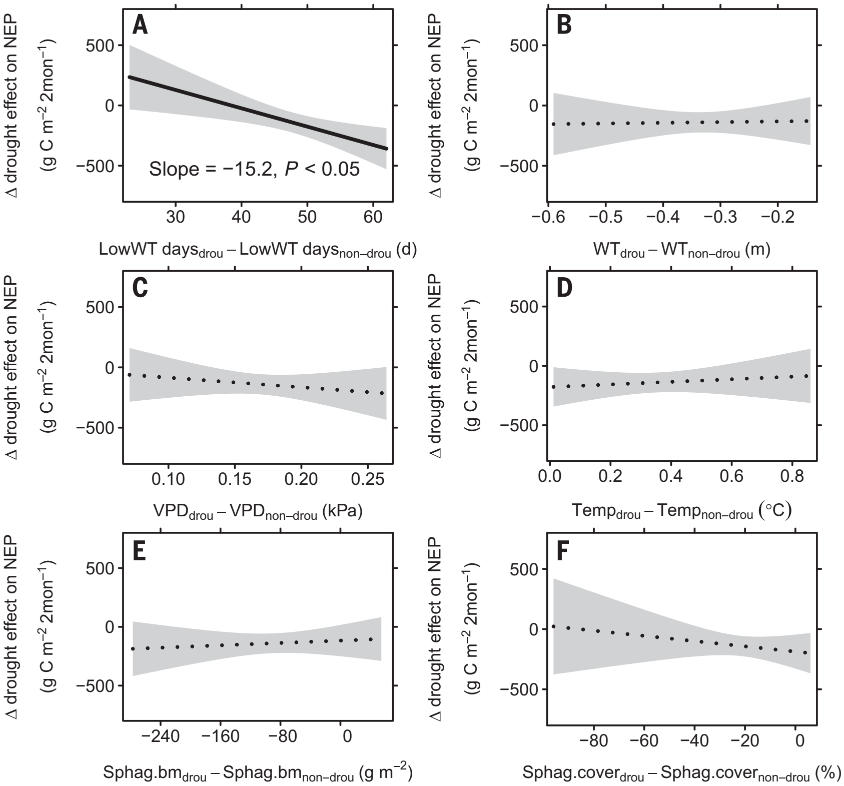

Fig. 2. Difference in drought effects on NEP between aCO_2 and eCO_2 treatment as related to various predictors. The difference, denoted by Δdrought effect on NEP, depends on drought-induced changes in (**A**) number of low-water-table (LowWT, below −0.25 m) days, (**B**) WT, (**C**) VPD, (**D**) temperature (Temp), (**E**) *Sphagnum* biomass (Sphag.bm), and (**F**) *Sphagnum* coverage (Sphag.cover), respectively. The fitted lines indicate the estimated effect of each predictor while controlling all other predictors. Solid lines indicate significant effects, and dashed lines indicate insignificant effects, with a significance level set at α = 0.05. The shaded bands indicate 95% CIs.

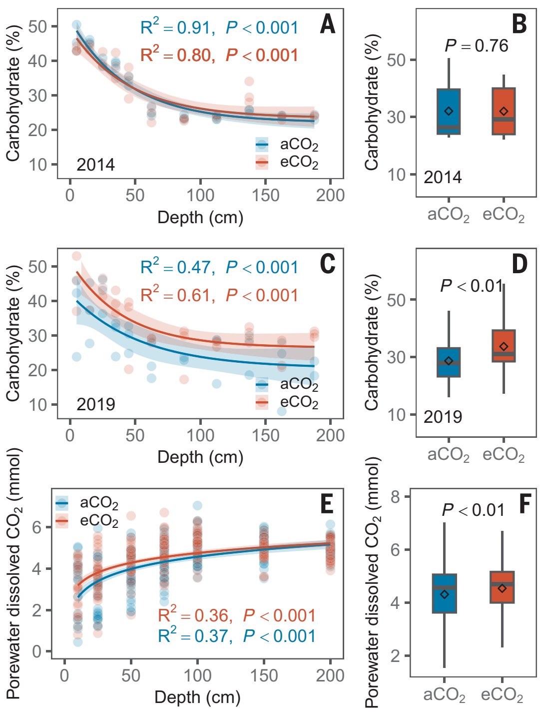

Fig. 3. Carbohydrate and porewater dissolved CO_2 concentrations in peat soil under aCO_2 and eCO_2. (**A** to **D**) Depth profiles of carbohydrate concentrations in [(A) and (B)] 2014 (before the eCO_2 treatment) and [(C) and (D)] 2019 (after the eCO_2 treatment). (**E** and **F**) Depth profile of porewater dissolved CO_2 concentrations between aCO_2 and eCO_2. The lower and upper boundaries of the boxplots indicate the 25th and 75th quartiles. The center lines indicate the median values, the rhombus-shaped points inside the boxes indicate the mean values, and the whiskers indicate 1.5 times the IQR. The fitted lines indicate regressions, and the shaded areas indicate 95% CIs.

structures (*52*). In such conditions, eCO_2-induced premature leaf senescence and abscission, along with excessive stomatal closure, can intensify the negative impact of drought on C uptake (*53*, *54*). Ridge regression analysis, which accounts for collinearity among drought-induced changes in all these potential causal variables (the number of low-water-table days, WT, VPD, temperature, and *Sphagnum* biomass and coverage), further supported these results (fig. S6). The differences in C flux responses to drought between aCO_2 and eCO_2 were not caused by differential drought responses of these factors because these responses were similar (figs. S7 and S8) and did not significantly differ between the two CO_2 treatments (figs. S9 to S11). Overall, with greater water table decline and an increased number of days with low water table, warming and eCO_2 jointly promote C release and suppress C uptake, exacerbating the decline in NEP during extreme drought.

Mechanisms driving amplified C loss under warming during drought

Under both CO_2 treatments, warming significantly amplified the drought-induced reductions in NEP. The temperature sensitivity of this response was 77.1 g C m^{-2} °C^{-1} under eCO_2, which is significantly greater than the 20.3 g C m^{-2} °C^{-1} under aCO_2 ($P < 0.001$) (Fig. 1). Warming can directly exacerbate peatland C loss during drought by shifting plant and soil fungal communities and enhancing the activity of C-degrading enzymes, which stimulates decomposition of recalcitrant deeper peat, as shown in many studies (*30*, *55*–*57*). Under nondrought conditions, it has been estimated that a 1°C increase in temperature reduces NEP by 17.0 [95% confidence interval (CI): 8.0 to 26.0] g C m^{-2} $year^{-1}$ across 16 northern peatland sites, which is comparable with the 24.6 (95% CI: 17.6 to 33.5) g C m^{-2} $year^{-1}$ reduction observed in the SPRUCE site (*58*). In addition, warming strongly amplifies drought-induced water table decline (fig. S9), exposing more peat to aerobic decomposition. A study showed that a water table decline of >0.3 m can strongly accelerate microbial respiration by 123% across global boreal peatlands (*43*). In our study, although warming did not significantly alter drought's effects on other variables (figs. S10 and S11), it significantly enhanced the water table decline and the number of low-water-table days during drought (fig. S9). Further analysis showed that warming-aggregated water table decline significantly contributed to warming-amplified increase in ER and decrease in NEP during drought (fig. S12). Moreover, warming promotes substrate availability for microbial decomposition in peatlands (*57*, *59*, *60*), which in combination with drought further accelerates peat soil C loss. Specifically, at the SPRUCE site, warming strongly promoted shrub fine-root growth by 1.2 km m^{-2} $year^{-1}$ °C^{-1} in 2016 and by 2.54 km m^{-2} °C^{-1} during the growing season (June to October) of 2017 (*61*). Increased belowground C allocation and root-derived labile metabolites primarily contributed to peat C release under warming (*31*, *49*, *50*, *62*). All of these processes will lead peatlands to lose more C under warming during extreme drought events.

Implications

These findings support our first hypothesis that warming intensifies peatland C loss during extreme drought events by enhancing microbial decomposition and lowering the water table. However, contrary to our second hypothesis, eCO_2, which typically mitigates drought impacts in upland ecosystems, exacerbated C loss in peatland by providing more substrate for decomposition and suppressing C assimilation under extreme drought and warming (*44*–*47*, *53*, *54*, *60*, *63*–*66*). The exacerbated peatland C loss during extreme drought under warming and eCO_2 (228.6 ± 56.8% and 381.9 ± 83.4% of the control at +9°C under aCO_2 and eCO_2, respectively) far exceeds that observed under current climates. This suggests that peatland C sinks may become increasingly vulnerable to future climate extremes.

In this study, the extreme drought period was defined on the basis of ambient water table dynamics. Whereas ambient plots exhibited water table drawdown and recovery during this period, warming plots experienced deeper and more prolonged water table drawdown without recovery during this period, likely because of higher VPD and evapotranspiration. This divergence explains the greater C loss under warming and eCO_2, underscoring that future droughts and their impacts could be much more severe than under the current climate. Our current analysis excluded NEP responses during the recovery phase under warming because it extended beyond the extreme window defined by ambient conditions. If the water table recovery phases were considered, the delayed recovery phases may cause more C loss under warming and eCO_2. Therefore, the recovery phase warrants further investigation (*10*, *26*).

Whether the warming- and eCO_2-amplified drought effects on C loss are short- or long-term remains an open question. Drought temporarily increases aerobic conditions, enhancing decomposition. However, when the water table recovers, peat returns to anaerobic conditions that slow decomposition. Moreover, much of the labile C may have already been decomposed during drought, potentially limiting post-drought decomposition. If drought persists, shifts in plant communities and organic C inputs could introduce new feedbacks that alter photosynthesis and decomposition over longer timescales (*67*, *68*). Whereas our short-term observations show that warming and eCO_2 immediately amplified C loss under extreme drought, the long-term impacts will depend on ecosystem responses to drought duration, frequency, and the combined effects of warming and eCO_2 (*67*, *68*).

Undisturbed northern peatlands are weak net C sinks, with long-term C accumulation rates ranging from 3 to 80 g C m^{-2} $year^{-1}$ over the past millennium (*69*), which is comparable with the 8 to 82 g C m^{-2} $year^{-1}$ measured at the SPRUCE site (*70*, *71*). This short-term NEP loss during the extreme drought event at +9°C under eCO_2 would erase 9.0 to 92.1 years of net C accumulation at the SPRUCE site, or potentially 9.2 to 245.5 years in other northern peatlands. Our study did not quantify drought impacts on methane (CH_4) emissions because it accounts for only a small fraction (7%) of ecosystem C exchange in northern peatlands (*72*) and typically approaches zero under drought condition when the water table drops to approximately −0.2 to approximately −0.3 m (*42*, *67*, *73*). Thus, it likely contributes little to net C loss during extreme drought. Consistent evidence from peatland studies shows that the increased CO_2 emission in response to drought and water table drawdown overwhelmingly outweighed the cooling effect from a reduction in CH_4 production, yielding a net warming effect (*42*, *74*, *75*). As extreme drought events become more frequent, our findings suggest that episodic C losses during the short-term droughts may substantially undermine long-term peatland C sequestration under future climate scenarios and pose a greater threat to the global C balance than current climate-based projections suggest.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adv7104
Materials and Methods; Figs. S1 to S17; Tables S1 to S3; References (*78*–*124*);
MDAR Reproducibility Checklist

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