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INCREASING IMPACTS OF EXTREME DROUGHTS ON VEGETATION PRODUCTIVITY UNDER CLIMATE CHANGE

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Abstract: Terrestrial gross primary production (GPP) is the basis of food production and vegetation growth globally[1], and plays a critical role in regulating atmospheric CO_2 through its impact on ecosystem carbon balance. Even though higher CO_2 concentrations in future decades can increase GPP[2], low soil water availability, heat stress, and disturbances associated with droughts could reduce the benefits of such CO_2 fertilization. Here we analyzed outputs of 13 Earth System Models (ESMs) to show an increasingly stronger impact on GPP by extreme droughts than mild and moderate droughts over the 21st century. Due to a dramatic increase in the frequency of extreme droughts, the magnitude of globally-averaged reductions in GPP associated with extreme droughts was projected to be nearly tripled by the last quarter of this century (2075–2099) relative to that of the historical period (1850–1999) under both high and intermediate greenhouse gas emission scenarios. In contrast, the magnitude of GPP reduction associated with mild and moderate droughts was not projected to increase substantially. Our analysis indicates a high risk of extreme droughts to the global carbon cycle with atmospheric warming; however, this risk can be potentially mitigated by positive anomalies of GPP associated with favorable environmental conditions.

The terrestrial biosphere absorbed ~30% of anthropogenic carbon emissions from fossil fuels during 1990–2007[3], making it a critical component of the global carbon sink that mitigates fossil fuel CO_2 emissions and associated climate warming. GPP is a measure of fixation of CO_2 into an ecosystem through photosynthesis and plays a key role in the net carbon balance of the terrestrial biosphere and the terrestrial CO_2 absorption. However, despite our knowledge of CO_2 fertilization effects on plant productivity[2], the future trend of GPP under elevated CO_2 levels remains highly uncertain due to the impact of many factors such as nutrient limitation[4] and increasing frequency and intensity of drought[5]. Drought is already the most widespread factor affecting GPP[6] via direct physiological impacts such as water limitation and heat stress[7], and through its indirect impacts on increased frequency and intensity of disturbances such as fire and insect outbreaks[8] that release large amounts of carbon back into the atmosphere. In agreement with such trends, several modeling studies have showed an increasing risk of a greater frequency and intensity of droughts in many regions during the 21st century[9-12], which could affect the magnitude of future GPP and lead to high uncertainty in projecting the future of terrestrial carbon sink. Previous studies have assessed the importance of different climate factors for carbon flux extremes[13,14], but few studies have specifically quantified future drought impacts on GPP at the global scale.

To better understand how future drought will affect GPP at the global scale, we analyzed the climate and GPP projections from 13 ESMs in the Coupled Model Intercomparison Project Phase 5 (CMIP5)[15]. The models were selected based on the criteria that they reported both soil water content at different depths and GPP, to quantify the potential impacts of droughts on future terrestrial GPP. Given that plant responses to water stress depend on their historical climate conditions[16], we defined location (i.e., grid cell for ESMs) and model-specific droughts during the historical period of 1850–1999 as months when plant accessible soil water (PASW: vertical integral of soil water weighted by the fraction of roots in a soil column at different depths) was less than the 10th percentile for each location. These percentile-defined droughts may not have an impact on GPP at very wet sites, therefore, we only used the 10th percentile to define droughts if GPP during these drought months was significantly lower (with a significance level of 0.01) than that of the non-drought months (see Methods and Extended data Fig. 1 for details). We classified droughts into extreme, moderate, and mild so that PASW was less than the 2nd percentile during extreme droughts, between the 5th and 2nd percentiles during moderate droughts, and between the 10th and 5th percentiles during mild droughts. Projected future droughts were sorted into these categories using the grid-cell-, model-, and month-specific historical simulations. The drought-associated change in GPP was calculated based on the deviations (or anomalies) of GPP from the mean for each month of a specific location during 1850-2099 (See Methods and Extended data Fig. 1 for details). Positive deviations from the mean indicate that droughts stimulate GPP and negative deviations indicate that droughts reduce GPP.

Our analysis showed that drought events defined by low PASW were projected to become more frequent under future climates (Fig. 1). The frequency of extreme droughts per year was projected to increase by a factor of ~3.8 (p-value < 0.001) under the high greenhouse gas emission scenario (RCP 8.5[15]) and by a factor of ~3.1 (p-value < 0.001) under the intermediate greenhouse gas emission scenario (RCP 4.5[15]) (Fig. 1a, b) during 2075–2099, compared to the historical period of 1850–1999. The mean frequency of moderate droughts per year was projected to increase by a factor of ~1.2 (not significant with p-value > 0.2) under scenario RCP8.5 (Fig. 1d) and by a factor of ~1.5 (p-value < 0.01) under scenario RCP4.5 (Fig. 1c). One reason for the relatively lower increase of moderate drought frequency under scenario

RCP8.5 in comparison to scenario RCP 4.5 was that drought events became more extreme under scenario RCP8.5 and thus there was a smaller proportion of moderate drought events under this scenario (Extended data Fig. 2). These droughts were widely distributed with particularly high risks for the Amazon, South Africa, Mediterranean Basin, Australia, and southwest USA (Fig. 2). The risk of mild droughts did not change significantly in the future (Fig. 1e, f). The drought events were typically associated with low humidity (Extended data Fig. 3), low precipitation (Extended data Fig. 4), high temperature (Extended data Fig. 5), high radiation (Extended data Fig. 6), and increased carbon release from fire disturbances (Extended data Fig. 7).

The magnitude of annual GPP reductions associated with droughts was also projected to increase substantially in the future (Fig. 3). In terms of absolute carbon fluxes, the magnitude of forecasted mean reductions in global GPP associated with droughts will rise from ~2.8 Pg C per year during 1850–1999 to ~4.5 and ~4.7 Pg C per year (p-value <0.01) during 2075–2099 under emission scenario RCP8.5 and RCP 4.5, respectively (Extended data Fig. 8). Drought-associated reductions in GPP (Figs. 3 and 4) can arise in two main ways: 1) via an increased intensity of droughts (in terms of GPP impact), or 2) via an increased drought frequency. Our analysis showed that the ensemble mean of absolute GPP reduction per drought event was not projected to be significantly larger in the future (Extended data Fig. 9). This could result from the effect of CO_2 fertilization for the both drought and non-drought months (see next paragraph for details). Therefore, the increasing impact of drought upon GPP mainly resulted from the increased frequency of drought events. Due to the relatively large increase in the frequency of extreme droughts (Fig. 1), the magnitude of GPP reductions associated with extreme droughts increased much more than that associated with moderate and mild droughts in the future (Fig. 3). Specifically, the magnitude of annual GPP reduction associated with extreme droughts during

2075–2099 was projected to increase by a factor of ~2.9 (p-value < 0.001) and ~2.7 (p-value < 0.001) under emission scenarios of RCP8.5 and RCP4.5, respectively (Fig. 3 a, b), compared to their historical mean values during 1850–1999. In contrast, no significant increase in the magnitude of mean GPP reduction was detected for mild and moderate droughts except for the moderate droughts under RCP4.5 (Fig. 3 c-e). Therefore, the proportion of total GPP reduction contributed by extreme droughts was projected to increase from ~28% during 1850–1999 to ~56 and 49% during 2075–2099 under emission scenarios RCP 8.5 and RCP4.5, respectively (Extended data Fig. 10). The projected GPP reductions associated with droughts were correlated with changes in several environmental drivers including PASW, temperature, humidity and radiation, and vegetation states with each variable contributing ~10–30% on average (Supplementary Fig. 1 and Supplementary Fig. 2).

The GPP reduction associated with droughts can be viewed in the context of rising GPP under future CO_2 fertilization, which was included in all selected Earth system model projections. Due to CO_2 fertilization and higher temperature for high latitudes, the globally-averaged mean GPP was projected to be ~50% and ~31% higher for year 2075–2099 compared to the historical period (1850–1999) under emission scenarios of RCP 8.5 and RCP 4.5, respectively (Supplementary Fig. 3). Similarly, the GPP in drought periods was also projected to increase significantly for mild and moderate droughts (p-value < 0.02) but not significantly for extreme droughts (Supplementary Fig. 4). To better understand the drought impacts in relative terms, we calculated the impacts of droughts as the percentages reduction in GPP associated with droughts. The percentage reduction averaged across all models showed no significant change during 2075–2099 compared to the historical period during 1850–1999 under RCP 8.5 (Supplementary Fig. 5 a). Under the emission scenario of RCP 4.5, percentage reduction of GPP by droughts was projected to have a slight increase from ~1.8% per year during 1850–1999 to ~2.3% per year (p-value < 0.01) in 2075–2099 (Supplementary Fig. 5b). Relative to RCP 4.5, the lower percentage reduction in GPP during 2075–2099 under RCP 8.5 could result from the beneficial impact of higher CO_2 concentrations on plant production during moderate and mild droughts (e.g., higher photosynthetic rate and increased water use efficiency with lower stomata conductance[2]) (Supplementary Fig. 6 c-e). For both mild and moderate droughts, the magnitude of percentage reduction in GPP decreased except for moderate drought under RCP4.5 (Supplementary Fig. 6 c-e). However, for extreme droughts, the percentage reduction in GPP was projected to be doubled (p-value < 0.001) under both emission scenario RCP 8.5 and RCP 4.5 (Supplementary Fig. 6 a, b). This suggests that the magnitude of extreme-drought-associated GPP reduction increases faster than the mean GPP in the future.

There was a large latitudinal variation in the projected impact of drought on GPP. The drought impacts on GPP for years 2075–2099 (measured by the grid-cell-specific GPP reduction relative to the historical period of 1850–1999) were much larger in tropical and temperate regions and smaller at high latitudes (Fig. 4; see Supplementary Fig. 7 for a reference over years 1975–1999). The uncertainty was also relatively lower for tropical and temperate regions as measured by the relative amount of deviation from the ensemble mean (Supplementary Fig. 8 and Supplementary Fig. 9). The large increase in the magnitude of drought-associated reduction in GPP projected for tropical and temperate regions (Fig. 4) is in agreement with recent observations of drought-associated vegetation changes in Europe[17], the Amazon basin[18], Western US[19,20], and the global assessment of drought-induced plant production reduction during 1999–2009 using remote-sensing-based estimates[21]. The small impacts of droughts on GPP at high latitudes could result from their relatively low GPP and beneficial consequences of higher temperature (Extended data Fig. 5) and radiation (Extended data Fig. 6) during the drier months in these colder regions[22], where relatively high antecedent soil moisture buffers vegetation against stress-inducing drought levels despite experiencing statistically dry conditions. However, this projection of small GPP reductions at high latitudes could be too optimistic given that all the current ESMs do not explicitly consider insect dynamics, which are influenced by drought and warming climate and have substantial impacts on regional to global carbon cycles[23,24]. Long-term observational data also showed that drought had already led to substantial tree mortality across Canada from 1963–2008[25].

The ESMs projected not only an increase of mean GPP in the future due to CO_2 fertilization (Supplementary Fig. 3), but also an increase of variability in GPP (Supplementary Fig. 10). This suggests that magnitude of both positive and negative anomalies around the mean of GPP will increase in the future[14]. The GPP reduction associated with drought represents one of the key drivers of negative abnormalities for the simulated GPP in ESMs; however, at global scale, these negative anomalies could be mitigated by the positive anomalies of GPP related to wet conditions, favorable temperature and radiation, and enhanced water use efficiency due to elevated CO_2 concentration[2]. Zscheischler et al[14] pointed out that the dominance of large negative carbon extremes (e.g., deviation of GPP from the mean) could be changed toward dominance of large positive carbon extremes in GPP in the 21st century. Thus, it is possible that the high risk of increasing impact of extreme droughts on GPP could be mitigated by the positive impacts on GPP in the future under favorable environmental conditions of temperature, soil moisture and radiation.

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Methods

We selected 13 ESM simulations (Supplementary Table 1) from CMIP5 archive, based on the criteria that they reported both soil water at different soil depths and GPP. There are multiple simulations for each ESM under each specific greenhouse gas emission scenarios. In this study, we selected only the first reported simulation for each model, given that multiple inclusions of the same model might lead to its over-representation in our analysis[26]. We also collected additional climate variables including precipitation, radiation, temperature and relative humidity to identify the deviations in climate for drought months from the same CMIP5 archive. In this study, we only considered two emission scenarios: RCP8.5 and RCP4.5. This was justified by the fact that these scenarios generally capture the potential range of future greenhouse gas releases and that fewer simulations are available for other emission scenarios.

There are many ways to define droughts[11]. Because our goal was to understand impacts of drought on GPP, we used plant accessible soil water (PASW) as an indicator of drought. PASW was defined as the sum of soil water weighted by the fractions of plant roots at different soil depths (see Supplementary Note 1 for details). Because drought tolerance of plants depends on their historical climate conditions[16], we defined droughts based on the site-specific PASW. Specifically, we defined a month in a specific year as a month of mild, moderate, and extreme drought if its PASW was less than (or equal to) the 10^{th} but larger than the 5^{th} percentile, less than (or equal to) the 5^{th} but large than the 2^{nd} percentile, and less than (or equal to) the 2^{nd} percentile for the same month during 1850–1999, respectively (Extended data Fig. 1a). These percentiles were then used to identify months of different levels of droughts during 2000–2099 based on the projected PASW. Even if PASW of a certain month was relatively low (e.g., $<10^{th}$ percentile) for a specific year, it may not have an impact on plant production if the site was very wet. Thus, we used these percentiles to define droughts only if GPP values of a specific month for the years with PASW less than the10th percentile were significantly lower than the rest of years during 1850–2099 (see Supplementary Note 1, Supplementary Fig. 11, and Supplementary Fig. 12 for details).

In most models, each grid cell can contain more than one plant functional type (PFT) with differing root distributions. Ideally, we could have defined droughts based on whether the PASW of a PFT had a significant impact on the PFT-specific GPP; however, the CMIP5 database only has a single total GPP for each specific grid cell. In this study, droughts were thus defined by PASW of different PFTs as long as GPP during the defined drought months was significantly lower than that during non-drought months (see Supplementary Note 1 for details of statistical tests). This does not affect our analysis because all the droughts defined by PASW of different PFTs had a significant impact on the lumped GPP. If a specific month was set as drought month by PASW of multiple PFTs, however, we defined the drought category based on the PASW of the PFT that had the most significant impact on GPP (see Supplementary Note 1 for details).

To quantify drought impacts on GPP, we first fitted a smooth spline over noisy simulations of GPP for a specific month (e.g., May) during 1850–2099 (Extended data Fig. 1b). See Supplementary Note 2 for details of smooth spline estimations. This spline was then used to represent the mean GPP for the month of interest. For each drought month, the deviation (or anomaly) of its GPP from the estimated spline was used to quantify the monthly impact of drought on GPP (Supplementary Note 3 and Extended data Fig. b). Finally, we summed these deviations across months and spatial locations to estimate impacts of the drought on GPP at the global scale. The corresponding standard errors were estimated based on the standard errors of the estimated spline (see Supplementary Note 2 for details). Statistical tests were used to test for significant differences in drought risks and associated GPP reductions (see Supplementary Note 5 for details). Our approach might underestimate drought impacts, because drought-associated GPP reduction could plausibly extend past the end of the duration of drought defined based on soil moisture[13,27]. Further studies based on specific model experiments are needed to identify these lag impacts, because it is difficult to confirm if the follow-on reductions in GPP result from the lag effects of droughts or other environmental condition changes (e.g., low radiation) in the CMIP5 archive.

It is important to point out that the PASW is only one indicator of drought. The impact of droughts on GPP can be attributed to different climate variables such as temperature, humidity, radiation, precipitation, and PASW, and to different vegetation states such as PFT compositions, height, and leaf area index. To understand the importance of different climate variables and vegetation states on GPP reductions associated with droughts, we fitted multilinear regressions to estimated GPP deviations with explanatory variables of PASW, daily temperature, incoming solar radiation, relative humidity, and mean GPP (as an indicator of overall vegetation status) for all the drought events for a specific month for the 25-year periods during 1850–2099 (see Supplementary Note 4 for details).

Data Availability

The ESM output data that support the findings of this study are available from the CMIP5 site (https://esgf-node.llnl.gov/projects/cmip5/).

Code availability

The processing R codes are available from corresponding author upon request.

METHODS REFERENCES

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ENDNOTES

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Author Contributions

All authors contributed to the manuscript writing. CX and NGM initially designed the experiment. CX implemented the analysis. LW helped data exploration for evaluating the results; RAF, SS, BOC and RM provide suggestions for improvement of the experimental design and analysis. EW provided support on water limitation functions and PFT mapping on GFDL and NOAA models.

Competing Interests statement

We declare that no competing interests are present in the manuscript.

Figure legends

Fig. 1 Temporal changes in annual drought frequency relative to the historical period of 1850–1999. The relative frequencies were calculated on a model-specific basis, dividing the projected mean annual drought frequency (drought events/year) for a specific period (e.g., years 2075–2099) by that over the historical period. Values <1 indicate that the drought frequency decreases while values >1 indicate that the drought frequency increases compared to the historical period. The P-values were calculated using the bootstrap sampling (see Supplementary Note 5.2 for details) to test if the mean frequency across different models during 2075–2099 were significantly higher than the historical period. The gray horizontal line represents the ensemble mean for 2075–2099. See Supplementary Table 1 for the abbreviations of 13 selected Earth system models.

Fig. 2 Spatial distribution of drought frequency during 2075–2099 relative to the historical period of 1850–1999. The relative frequencies were averaged over the ensemble of 13 Earth system models. They were calculated on a model- and grid-cell-specific basis, dividing the mean drought frequency per year (drought events/year) during 2075–2099 by that over the historical period. Values <1 indicate the drought frequency decreases while values >1 indicate that the drought frequency increases compared to the historical period. The frequencies projected by different models were interpolated to a reference spatial resolution [1.125^{o} (longitude) x 0.9375^{o} (latitude)] for mapping purposes.

Fig. 3 Temporal changes in GPP anomalies associated with droughts relative to the historical period of 1850–1999. The relative anomalies were calculated on a model-specific basis, dividing the mean annual GPP anomaly associated with droughts (kg C/m^2/ year) for a specific period (e.g., years 2075–2099) by that for the historical period (see Methods and

Supplementary Note 3). They were multiplied by (-1) to indicate that droughts decrease GPP, with -1 indicating the reference drought-associated GPP anomaly for the historical period. Hence, values < -1 indicate that the magnitude of GPP reduction becomes larger relative to the historical period, while values > -1 indicate that the magnitude of GPP reduction becomes smaller. The dotted line shows the mean relative anomaly during 2075–2099 across all models. The P-values were calculated using the bootstrap sampling (see Supplementary Note 5.2 for details) to test if the mean magnitude of GPP reduction during 2075-2099 across different models becomes significantly larger than that during the historical period. See Supplementary Table 1 for the abbreviations of 13 selected Earth system models.

Fig. 4 Spatial distribution of GPP anomalies associated with droughts during 2075–2099 relative to the historical period of 1850–1999. The relative anomalies were averaged over the ensemble of 13 Earth system models. They were calculated on a model basis, dividing the grid-cell-specific mean annual GPP anomalies (kg C/m^2/ year) during 2075–2099 by the global mean annual GPP reduction (kg C/m^2/ year) for the historical period. The relative anomalies were multiplied by (-1) to indicate that droughts decrease GPP, with -1 indicating the reference global mean GPP reduction for the historical period. Hence, values < -1 (shades of red) indicate that the magnitude of GPP reduction was larger than the global mean GPP reduction during the historical period, while values > -1 (light blue) indicate that the magnitude of GPP reduction was smaller. The drought-associated changes in GPP projected by different models were interpolated to a reference spatial resolution [1.125 ^{o} (longitude) x 0.9375^{o} (latitude)] for mapping purposes.