Review

Responses of Forest Carbon Cycle to Drought and Elevated CO$_2$

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Abstract: Forests play a pivotal role in mitigating global warming as an important carbon sink. Recent global greening trends reflect a positive influence of elevated atmospheric CO$_2$ on terrestrial carbon uptake. However, increasingly frequent and intense drought events endanger the carbon sequestration function of forests. This review integrates previous studies across scales to identify potential global trends in forest responses to drought and elevated CO$_2$ as well as to identify data needs in this important research field. The inconsistent responses of ecosystem respiration to drought contributes to the change of forest net CO$_2$ exchange, which depends on the balance of opposite effects of warming and water stress on respiration. Whether CO$_2$ fertilization can offset the effects of drought remains controversial, however, we found a potential overestimation of global CO$_2$ fertilization effects because of increasing water stress and other limitations such as light and nutrients (N, P) as well as the possibility of photosynthetic acclimation.

Keywords: drought; elevated CO$_2$; carbon cycle; water use; photosynthesis

1. Introduction

Forest ecosystems play a key role in the land-atmosphere system and provide wide ecological services and socio-economic benefits, including forest products, water regulation, biodiversity, soil protection, spiritual and inspirational needs, recreational activities and aesthetic value [1]. Additionally, climate is influenced and regulated by the interaction of forests and atmosphere through the exchange of energy, water, CO$_2$ and other chemical compounds. Forests capture atmospheric CO$_2$ and sequester it into their biomass and soil, and then release oxygen back to the atmosphere, which is the buffer against global warming. Forty-five percent of the terrestrial carbon is stored in forest biomass, organic matter and soil, which is one of the largest global carbon pools [1]. Terrestrial ecosystems take up around 3 petagrams (Pg) of carbon emitted by human activities per year and capture nearly 30% of the CO$_2$ released by logging and the combustion of fossil fuel [2]. However, small shifts in the balance of forest ecosystem photosynthesis and respiration can lead to huge changes in the forest carbon cycle [3]. For example, elevated atmospheric CO$_2$ promotes the rate of plant photosynthesis and enhances water use efficiency (WUE) by reducing stomatal conductance, which can offset part of carbon emissions without more water consumption [4].

The increase of plant photosynthetic rate by CO$_2$ fertilization effects is considered one of the potential reasons for the observed global greening trends [5]. Higher WUE under elevated atmospheric CO$_2$ makes plants more tolerant to water stress [6], however, frequent occurrence of extreme droughts and heat stress lead to the decline of forest productivity and biomass accrual by widespread tree mortality and wildfires [7]. The balance between drought-induced forest carbon loss and enhanced carbon uptake by CO$_2$ fertilization depends on the severity and duration of droughts. The extent to which climate change affects forest carbon uptake and the interaction of drought and elevated CO$_2$ on plant stress resistance is still unclear. We review the current understanding in the response of the forest

carbon cycle to droughts and elevated CO_2 and highlight a research gap in the interaction of drought and elevated CO_2 on forest ecosystems. Since the global warming and severity of extreme events will continue to increase if greenhouse gas emissions are unmitigated, understanding the implications of the capacity of forests to sequester carbon under climate scenarios remains a pressing and crucial need.

2. Drought and Forest Carbon Cycle

Multiple concepts and indices of drought are applied in drought-related studies, which reflects the inconsistent indicators used to identify drought events. Climate change exacerbates the frequency, intensity and duration of extreme droughts, which directly impairs the carbon sequestration function of forest ecosystems. We clarify the definition of drought and discuss forest carbon cycle feedback to drought below.

2.1. Drought Definition

Kelly Redmond [8] generally describes drought as 'insufficient water to meet needs'. The moisture of terrestrial ecosystems is primarily provided by precipitation, but water demand comes from numerous places, for example, plant transpiration, land surface evaporation, agricultural irrigation and urban water use [9]. Therefore, although studies related to terrestrial ecosystem responses to droughts have a long history, there is no unified or standard definition for drought. Instead, researchers have characterized and defined drought in various ways according to the impacts of drought. For instance, drought can be described as precipitation decrease, low soil moisture, low water flow and plants facing water stress compared with normal conditions [10]. Multiple drought indices have been widely used to quantitatively define drought events, such as the Standardized Precipitation Index (SPI), the Standardized Precipitation-Evapotranspiration Index (SPEI), the Palmer Drought Severity Index (PDSI) and the self-calibrate PDSI (sc-PDSI). These indices require diverse input data and reflect different concepts of drought. For example, the SPI calculation only requires the time series of precipitation but does not consider the impact of evapotranspiration. SPEI was developed to compensate for this absence, which uses the same statistical method as SPI, but the input precipitation data is replaced with the difference between precipitation and potential evapotranspiration data (which is related to air temperature). Moreover, indices which perform well in specific regions may be unsuitable for other regions with different climate patterns and topographic conditions. Eslamian et al. [11] indicate that the PDSI performs better in wide plains than other indexes, such as in the United States and Australia. The Surface Water Supply Index (SWSI) is more suitable for the less-flat mountainous region [11]. A review focused on drought definition indicates that studies often confuse drought with dry conditions [10]. They calculated the SPEI for a group of drought-related studies, which did not quantify drought with specific indices, and found that 50% of drought events in those studies were defined as a normal condition by the SPEI ($-1 <$ SPEI < 1). This surprising result may be attributed to the fact that the drought events in these studies had a shorter duration than the timescales of calculation [10].

Inconsistent definitions of drought may result in uncertainties in assessments of drought and drought-related ecological impacts. In addition to incorporating standard information (SPEI, PDSI, etc.) and statistically standardizing the definition of drought, it is also important to consider the response of ecosystems to drought. Smith [12] defined ecosystem-related extreme events as conditions in which changes in ecosystem functions and structures (such as productivity, nutrients, species composition and population) deviate from normal variability within a certain duration and area. Moreover, responses of ecosystems to extreme events include immediate and delayed effects [13], so the lagged response that happen after extreme events should also be considered.

2.2. Forest Carbon Cycle Feedbacks to Drought

Seventy-eight percent of the changes of global gross primary production (GPP) in the past three decades are related to extreme events, while drought events account for 60–90% of these climate extremes [14]. The water limitation and high air temperature directly affect the carbon cycle of forests through plant responses to stress. Resistance strategies of plants coping with drought include changes in plants physiological traits [15]. At the leaf level, plant responses to drought are reflected in the reduced stomatal conductance and changes in photosynthetic and respiratory rates, which directly affects the carbon exchange between vegetation and the atmosphere (Figure 1). Granier et al. [16] demonstrated that soil moisture is the dominant limiting factor for forest carbon exchange in the 2003 Europe drought event because the GPP and ecosystem respiration (Re) both dropped sharply when the relative extractable soil water was lower than about 0.4. Furthermore, the ecosystem feedbacks may aggravate the severity of drought because: (i) The evaporative cooling effect is reduced due to stomatal closure, so the high leaf temperature may cause heat stress; (ii) high-light stress aggravated by drought leads to the occurrence of photoinhibition or even photodamage; (iii) high temperature, high radiation and rising vapor pressure deficit (VPD) exacerbate drought by higher evapotranspiration [17].

Forest carbon uptake and sequestration can rapidly decrease after widespread tree mortality [18], and the impacts of the decline in forest net primary productivity (NPP) could last for decades. Moreover, the decomposition process of the remnant biomass and underground dead roots releases stored carbon back to the atmosphere (Figure 1c), which can transform forests from carbon sinks into sources. Tree mortality is usually induced by the combination of multiple driving factors such as climate stress, diseases related to pests and pathogens, the stand life histories and fires [19]. Drought may serve as an inducer of the death of trees that are already under stress. The complexity of these drought-induced death mechanisms of trees makes the monitoring of tree mortality challenging. McDowell et al. [20] proposed three hypotheses about the mechanisms of drought-induced plant die-off: (i) Hydraulic failure; (ii) carbon starvation, where water limitation-induced stomatal closure blocks carbon uptake; and (iii) biotic attack, where changes in populations of pests and pathogens under continuous warming lead to excessive tree damage and mortality. Hydraulic failure is considered to be the main factor leading to plant mortality related to drought [21,22]. The hydraulic failure hypothesis states that low soil water potential and soil hydraulic conductivity lead to an increase in the vapor pressure difference between leaves and atmosphere and the rising demand for evaporation. The xylem conduits and rhizosphere are filled with air so the plant hydraulic system cannot transport water from the rhizosphere to leaves resulting in plant tissues desiccation and death [20]. Drought-induced tree mortality directly influences the land-atmosphere interaction because of the loss of vegetation function of exchanging water, energy and carbon.

Literature reporting forest carbon cycle responses to drought events in the last two decades is summarized in Table 1. The main causes of forest carbon budget variations related to drought are summarized below. First, increased tree mortality induced by drought explains large forest carbon storage loss in North America [17,23–25] and the Amazon [26–28]. As an example, in the 2010 Amazon drought event, an estimated 2.2 Pg C storage was impacted [27] with a wider impact area than the 2005 event (1.6 Pg C [26]). This impact was mainly derived from the temporary suspension of biomass growth and tree mortality, which reversed the forest from a net carbon sink to source [27].

Second, studies from North America and Europe suggest drought duration and timing are crucial factors that affect the dynamics of forest carbon balance between gross primary productivity and ecosystem respiration [29–31]. For example, the increase of forest carbon uptake in a warm spring is eliminated by subsequent summer drought [29–32], and early warming-induced consumption of soil moisture may intensify the water stress and heating in summer [30]. In addition, the sensitivity of carbon flux to warming and drought varies among vegetation types [31,33]. Alaskan deciduous forests showed a much higher net carbon uptake during the growing season than evergreen forest because of leaf area increase

in warm spring, which enlarged the difference of response to summer drought between deciduous forests and evergreen forests [33]. This result indicates a bigger contribution of CO_2 uptake by deciduous forests in the northern hemisphere.
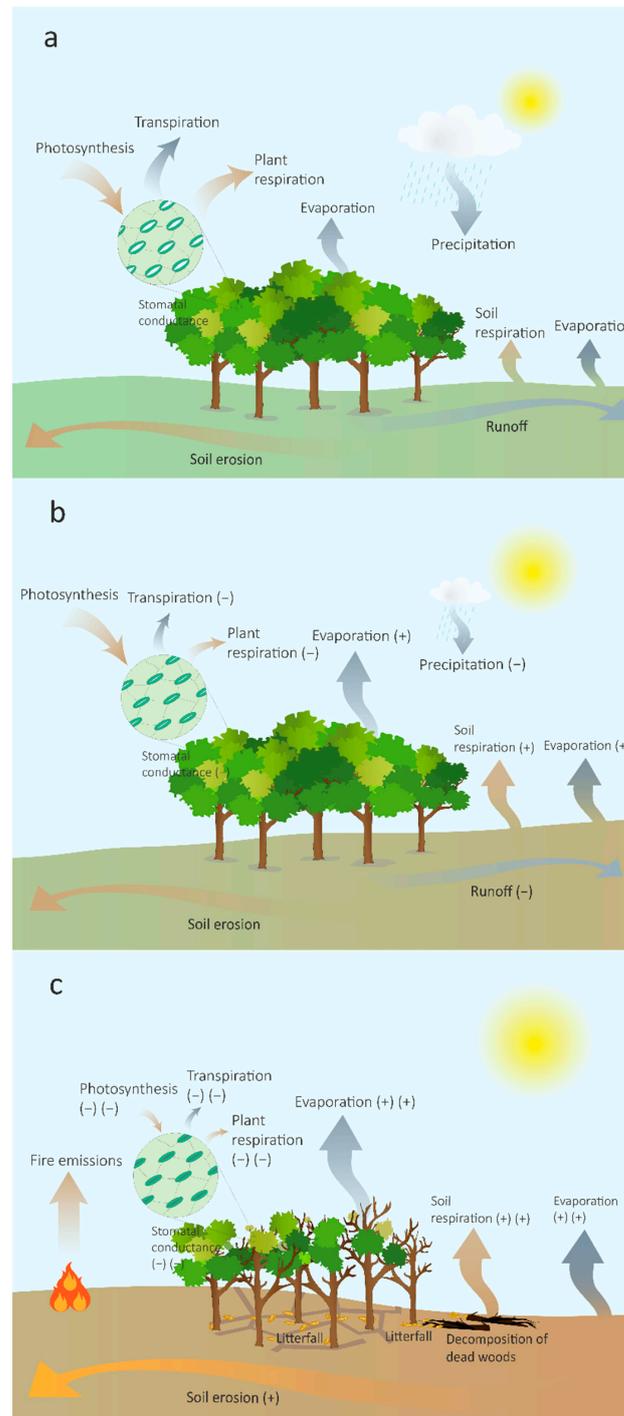
Figure 1. Forest carbon and water fluxes change as the intensity of drought increases. (**a**) Before drought events. (**b**) Moderate drought without tree mortality. (**c**) Severe drought with large biomass loss. Orange arrows show the carbon flux; blue arrows show the water flux. The magnitude of fluxes is indicated by the size of arrows. Numbers of (+) and (−) indicate that the degree of fluxes increase and decrease, respectively. Plant respiration includes leaf and stem respiration; soil respiration includes autotrophic soil respiration (roots) and heterotrophic respiration (litterfall, microbial community, soil organic matter, etc.).

Third, the response of ecosystem respiration is expected to contribute to the uncertainty of the net CO_2 exchange, because if Re and GPP decrease with a similar magnitude, the net primary productivity is expected to be unaffected by drought. The magnitude and direction of Re variation depend on duration and severity of drought and regional characteristics (such as soil moisture and vegetation types). Von Buttlar et al. [34] global study suggests that the direction of ecosystem respiration change depends on whether heat stress coincides with drought because heat and drought have the opposite impacts on Re. Re will keep stable if a warming-induced increase in Re is offset by water limitation. For example, ecosystem respiration in Alaskan forests increased during the 2004 summer drought because warming-caused increases in respiration exceeded the effects of limitations such as soil moisture and oxygen content [33]. Moreover, the European hot drought in 2003 led to a reduction in ecosystem respiration (autotrophic and heterotrophic respiration decreased) [16,35,36]. Ciais et al. [35] suggest that less carbon assimilation led to plant respiration decrease, and the negative effect of higher water stress on heterotrophic respiration exceed the positive effects of warming on it. Similar results were found in Lindroth et al. [37], they suggest that most forests in their study experienced a decline of net ecosystem productivity (decrease both in GPP and Re) in the 2018 summer drought across Northern Europe, and the forest carbon balance change was largely explained by decreased heterotrophic respiration and lack of precipitation.

Table 1. Summary of forest carbon cycle responses to drought events in recent two decades.

Location	Period	Forest Carbon Variations	Causes	Reference
North American boreal forest	20th Century	• Restricted carbon uptake	• Heat stress • Water deficit	Barber et al., 2000 [38]
Europe	2003	• Reduction of GPP • Reducing ecosystem respiration • Reduction of NPP	• Precipitation deficit • Extreme summer heat	Ciais et al., 2005 [35] Reichstein, M. et al., 2007 [36] Granier et al., 2007 [16]
Canada's boreal forests	2000–2003	• 2000 increase of NPP • 2002–2003 decrease of NPP	• 2000 warm spring and deep soil moisture available • 2002–2003 water deficit	Kljun et al., 2006 [29]
Interior Alaska	2002–2004	• Reduction of GPP • Increase of ecosystem respiration • Reduction of NPP	• Increased temperature • Increased vapor pressure deficit	Welp et al., 2007 [33]
Amazon	2005	• Total biomass carbon impact of 1.2 to 1.6 Pg • Total carbon impact of 2.2 Pg	• Water deficit	Phillips et al., 2009 [26]
Amazon	2005, 2010	• Total carbon impact of 2.2 Pg • The temporary pause of biomass growth • Loss of biomass	• Tree mortality • Heterotrophic respiration	Lewis et al., 2011 [27]
Aspen forests in North America	2009–2011	• Reduction in aboveground live biomass in aspen forests	• Tree mortality	Huang and Anderegg, 2011 [17]
Canada's boreal forests	1965–2005	• Loss of the biomass carbon sink • Slowness of tree growth • Reduction of NPP	• Water deficit • Tree mortality • Reduction of solar radiation	Ma et al., 2012 [23]
Congo rainforest greenness	2000–2012	• Decreasing greenness • Decrease of photosynthetic capacity	• Water deficit • Increased temperature • Increased photosynthetically active radiation	Zhou et al., 2014 [39]
Amazon	1985–2010	• Downtrend of carbon accumulation • Decreasing rates of aboveground biomass growth • Shorter carbon residence times	• Tree mortality	Brienen et al., 2015 [28]
United States	2012	• Increase of NPP during warm spring • Decrease of NPP during summer drought	• Warm spring • Soil moisture deficit	Wolf et al., 2016 [30]
Texas	2011	• Loss of 9.5% tree cover	• Tree mortality	Schwantes et al., 2017 [24]

Table 1. *Cont.*

Location	Period	Forest Carbon Variations	Causes	Reference
Global	Site-dependent	• Reduction of GPP and Re, neutral NPP response (drought without heat) • Reduction of GPP and NPP, increase of Re (drought with heat)	• Drought and heat	von Buttlar et al., 2018 [34]
California	2001–2015	• Loss of 188.4 Tg carbon storage	• Tree mortality • Wildfire	Sleeter et al., 2019 [25]
North American forests	Site-dependent	• Reduction of NPP in deciduous forests • Neutral NPP variation in conifer forests	• Seasons • Timing of drought	Xu et al., 2020 [31]
Northern Europe	Dry summer of 2018	• Reduction of GPP • Reducing ecosystem respiration • Reduction of NPP	• Precipitation deficit • Heterotrophic respiration	Lindroth et al., 2020 [37]
Site-dependent	Site-dependent	• Fast decrease of GPP • Increase of WUE	• Flash drought • High VPD • Low soil moisture	Zhang and Yuan, 2020 [40]
Europe	2018	• Reduction of GPP	• Decrease of soil relative extractable water content	Gourlez de la Motte et al., 2020 [41]
Europe	2018	• Decrease of net CO_2 uptake • Increase of WUE	• Low soil moisture	Graf et al., 2020 [42]
Europe	2018	• Reduction of GPP • Reducing ecosystem respiration	• Low soil moisture	Smith et al., 2020 [43]

3. Elevated CO_2 Effect on Plants and Ecosystem

Increasing global CO_2 emissions positively stimulate the terrestrial gross primary productivity. Previous research on plant response to elevated CO_2 has been developed across a range of scales, from leaf-level physiological experiments to satellite observations and the modelling of ecosystem response. We discuss CO_2 fertilization effects from the perspectives of plant physiology to ecosystem response below.

3.1. How Plants Respond to Elevated CO_2

Enriched atmospheric CO_2 concentration interferes with plant physiological processes by reducing plant stomatal conductance, increasing water use efficiency and simultaneously enhancing photosynthesis rate and light use efficiency [4]. However, the CO_2 fertilization effect is usually provisional since plants often acclimate to long-term elevated atmospheric CO_2 with lower photosynthetic capacity. Furthermore, CO_2 fertilization effects on plants may also be limited by other nutrients such as nitrogen (N) and phosphorus (P) [44].

3.1.1. Stomatal Conductance

The stomatal aperture is determined by the turgor pressure of the guard cell [45]. CO_2 enrichment stimulates the guard cell by changing the ion channel activities or the ion composition inside and outside the cell membrane [46]. The response of stomata to atmospheric CO_2 concentration varies among species, mainly owing to genetic traits and stomatal acclimation to humidity [4]. A reduced stomatal conductance (g_s) under the enriched CO_2 explains the decrease in leaf transpiration and the increase in water use efficiency, but it does not seem to limit photosynthesis. Whether reduced g_s restricts photosynthesis is indicated by the ratio of intercellular to atmospheric CO_2 concentration (Ci/Ca). The decrease in stomatal conductance appears to limit plant photosynthesis if the value of Ci/Ca in elevated CO_2 is less than that in normal ambient CO_2. However, Drake et al. [4] examined experiments with different species and found that there is no significant difference in Ci/Ca between plants grown in ambient CO_2 and elevated CO_2,

which proves that the reduced g_s does not inhibit plant photosynthesis but enhances the WUE of plants.

3.1.2. Photosynthesis

The mechanism of plant photosynthesis stimulation by elevated CO_2 is mainly driven by the activity of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Rubisco catalyzes the carboxylation reaction to fix CO_2 into 3-phosphoglyceric acid (3PGA) [47]. Since Rubisco has a low affinity for CO_2 carboxylation and is not saturated at current CO_2 concentration, elevated CO_2 can stimulate and promote the carboxylation reaction [4]. However, Rubisco can also catalyze the oxygenation reaction of Ribulose-1,5-bisphosphate (RuBP) and O_2, that is, the first step of photorespiration that inhibits photosynthesis by consuming light energy and releasing assimilated carbon [45]. The balance of carboxylation and oxygenation reactions depends on the ratio of O_2 to CO_2 concentration of the site of carboxylation. Elevated CO_2 stimulates carboxylation reactions and inhibits oxygenation reaction, promoting the process of photosynthesis. However, the affinity of Rubisco for CO_2 and the solubility of CO_2 (relative to O_2) decrease with increasing temperature, thus the increase in temperature will promote photorespiration [48]. The stimulating effect of elevated CO_2 on photosynthesis increases with the rising temperature, and CO_2 fertilization has a stronger effect with high temperature.

Compared with C3 plants, elevated CO_2 has no direct effect on the photosynthesis of C4 plants, because C4 plants have a mechanism which can avoid photorespiration. In FACE experiments, the response of C3 plants to elevated CO_2 is three times that of C4 plants [44]. Recent studies [49,50] argue that C4 plants benefit from elevated CO_2 indirectly by the interaction of decreased g_s and water stress, that is, the drought stress is mitigated by rising CO_2-induced higher water use efficiency.

3.1.3. Photosynthetic Acclimation

The photosynthetic rate is accelerated by short-term CO_2 increases, but plants may eventually adapt to elevated CO_2 atmosphere in the long-term. Plants grown in long-term elevated CO_2 will experience photosynthetic down-regulation, accompanied by higher concentrations of carbohydrates, lower concentrations of soluble proteins and Rubisco than those grown in the normal ambient atmosphere [4]. The stomatal acclimation to elevated CO_2 shows a significant downtrend in stomatal conductance, which is also associated with photosynthetic acclimation [45,51]. Nevertheless, the decline in g_s is not considered the dominant reason for the down-regulation of photosynthesis because there is no obvious difference in Ci/Ca between plants grown in elevated and ambient CO_2 [4,44]. The mechanism of acclimation of photosynthesis and stomata behavior is not completely understood, but there are several common possibilities. First, plants are unable to use extra carbohydrates produced by CO_2-stimulated photosynthesis, which then trigger the feedback mechanism that inhibits carbohydrate production at the source [4,45]. Second, the content and activity of Rubisco decrease under elevated CO_2 [4,52]. While there is no widespread agreement that photosynthesis will acclimate to elevated CO_2, it is hasty to consider photosynthetic acclimation as the eventual result of the plant response to elevated CO_2, especially at ecosystem scale.

3.1.4. Nutrient Availability

Rubisco requires a large amount of N investment and the activity of Rubisco play a key role in determining elevated CO_2 effects on photosynthesis rate. Therefore, the strength of CO_2 fertilization will be greatly reduced when other nutrients such as N are limited. There have been many experiments and studies supporting the hypothesis that CO_2 fertilization is limited by N availability [53–55]. When the sink strength of plants is limited due to N restriction, CO_2-stimulated excess photosynthate is more likely to trigger the feedback mechanism of plants that reduces products of photosynthesis from the source, thus leading to an earlier occurrence of photosynthetic acclimation [56]. The process of P affecting forest

carbon uptake is different from that of N. Ellsworth et al. [57] provide the evidence from FACE experiments that P potentially limits the effect of CO_2 fertilization, although their experiment is limited to forests consisting of single species. Terrer et al.'s [58] data analysis of 138 elevated CO_2 experiments shows that the strength of elevated CO_2 effect on 25% of global vegetation is primary constrained by P availability.

3.2. Ecosystem Responses to Elevated CO_2

Plant physiological response to elevated CO_2 at the leaf level has been supported by short-term individual experiments, however, extrapolation of these conclusions from individuals to ecosystems requires multiple data across scales. Over the past decades, research of plant responses to elevated CO_2 scaled up and increased in complexity. Large-scale open-top chambers (OTC) and FACE experiments with an open-air condition reflect plant responses to elevated CO_2 at the field level and extend the timescale of research, however, the incorrect data, experimental deficiencies (such as the unnatural increase of CO_2) and unsatisfactory future prediction needs still challenge the understanding of global-scale forest responses to climate change.

Satellite observations reveal the change in global vegetation on a scale of decades and there is a documented upward trend on vegetation cover in the northern hemisphere over the past two decades [59]. Recent evidence [60–63] indicates that in recent decades, this trend is probably attributed to a combined effect of the elevated CO_2, nutrients, water supply, solar radiation and socio-economic factors (such as land use change and reforestation). For example, according to Nemani et al. [60], global land NPP experienced a climate-induced increase between 1982 and 1999, which is probably due to solar radiation increase rather than CO_2 fertilization in the Amazon rainforest (accounting for 42% of total global NPP increase). Hickler et al. [64] analyze the drivers of the Sahel greening trend through ecosystem modelling and the output suggests that precipitation is the main cause of increased vegetation cover while CO_2 has only a small contribution. However, CO_2 fertilization is considered more obvious in areas where water is the primary limitation for vegetation growth because the increased WUE under elevated CO_2 mitigates water stress [5]. Donohue et al. [5] indicate that the prediction of CO_2-stimulated increase in maximum foliage cover is consistent with satellite observations, which suggests that CO_2 does play a key role in warm and arid area greening. Ukkola et al. [65] showed consistent results with Donohue et al., and they indicated that the WUE of vegetation in Australia increased over the past decades due to CO_2 fertilization. A new method, which scales up from leaf and canopy level, was developed by Ueyama et al. [66] to isolate elevated CO_2 effects from other effects and quantify the magnitude of vegetation response globally, and their results supported the effects of CO_2 enrichment on GPP increase and transpiration decrease.

Process-based models that involve mechanical process descriptions are feasibly to isolate global forest response to CO_2 fertilization from other drivers on a longer time scale (decades). Piao et al.'s [67] modelling studies based on ORCHIDEE suggest that 49% of the increase of leaf area index (LAI) in growing season in the northern hemisphere is contributed by atmospheric CO_2 (temperature and precipitation account for 31% and 13%, respectively). Ten carbon cycle models used for the IPCC were evaluated through statistical functions by Piao et al. [68] and their results show that every increase of 100 ppm CO_2 concentration contributes to 5–20% simulated NPP increase, which slightly exceeds the results from FACE experiments (13%). However, Wang et al. [69] indicated a decline in CO_2 fertilization effects from 1982 to 2015 based on observation datasets, which related to increased nutrient (N, P) limitations and water limitation. Their results suggest an overestimation of ecosystem response to elevated CO_2 by carbon cycle models, possibly associated to constraint factors, which restrict the ability of ecosystem responses, such as nutrient limitation, photosynthetic acclimation and soil moisture deficit.

4. Interaction of Drought and CO_2 Fertilization

Plant responses to elevated CO_2 and warming is reflected in the increase of photosynthetic rates and water use efficiency. Recent studies [49,50,70,71] suggest that the CO_2 fertilization effect on WUE partly eliminates water limitation during drought events, however, few reports have given explicit quantitative magnitude of the WUE effect. The extent to which extreme events such as drought that negatively affect the ability of vegetation to sequester carbon, and the degree to which the impact of drought can be offset by rising CO_2 remains unresolved and debatable. The ecosystem categories and drought intensity and duration are considered to determine the effects of higher water use efficiency on drought resistance. Figure 1 shows the fluxes of carbon and water under elevated CO_2 in different levels of drought intensity, exhibiting the responses of forests to diverse droughts.

Reduced stomatal conductance under elevated CO_2 may be able to limit water consumption at leaf level (Figure 1b), but the increased evapotranspiring leaf area attributed to rising biomass stimulated by elevated CO_2 may offset the effect of CO_2-induced stomatal response [72]. The sensitivity coefficient of ecosystem evapotranspiration (ET) to atmospheric CO_2 reflects whether biomass growth or lower stomatal conductance dominates ecosystem ET [65]. Ecosystem evapotranspiration response to elevated CO_2 may lead to soil moisture and atmospheric humidity variations, which is classified as an indirect response of ecosystems to elevated CO_2 [49]. This response varies greatly among ecosystems and species, such that there is not yet a consistent pattern that can describe it.

Evidence from gas exchange chamber experiments suggest that elevated CO_2 benefits to water efficiency will initially help resist desiccation. This benefit will gradually disappear under continued drought and heat, as VPD-induced stomatal closure will contribute to loss of CO_2 assimilation and increased respiration with leaf temperature leading to CO_2 loss (Figure 1c) [6]. The increase in air temperature and desiccation may reverse the CO_2-induced WUE increase. Reichstein et al. [73] suggest that the potential possibilities of stomatal closure led to ecosystem water use efficiency decreasing during drought. Although warming and elevated CO_2 are expected to benefit plant growth, warming-induced water stress will restrict the positive effects of CO_2 fertilization on photosynthesis [70]. Yuan et al. [74] indicate that the terrestrial GPP in the late 1990s experienced a continuous large-scale decline, while the vapor pressure deficit increased sharply during the same period, which offset the effect of CO_2 fertilization. Silva et al. [70] analyzed temperate and boreal forests in Ontario, Canada, by isotopic and dendrochronological methods, and showed that rising CO_2 did increase the water use efficiency, but forest tree growth experienced a widespread decline due to water limitation induced by warming, which suggests that the increase in WUE cannot offset the growth decline under warm drought. A positive case that CO_2 fertilization and warming reverses the negative effect of water limitation was found by Morgan et al. [50], who conducted FACE experiments in a semi-arid grassland with C4 grasses. However, their experiments only suggest the effective response of WUE to resist desiccation in grassland and did not cover other vegetation types. Furthermore, drought-induced tree mortality is an essential driver of forest carbon loss. Duan et al. [75] indicated that high temperature accelerates the process of plant hydraulic failure and death and the mitigative effect of elevated CO_2 is negligible, but their study is limited to tree seedling mortality.

Therefore, the combined effects of drought and CO_2 fertilization depend on the forest's ability to resist water limitation, which leads to whether the biomass growth is stimulated by atmospheric CO_2 or lost because of drought-induced tree mortality [18]. There is a concept of the "tipping point" for tropical forests, which indicates that forests will lose their storage carbon sharply when the global daily maximum temperature over the year increases to 32.3 °C, especially in drier forests where water is the primary limitation [18].

5. Conclusions and Outlook

Although we have recognized that drought events and CO_2 fertilization have critical impacts on the carbon cycle of forests, it is still challenging to figure out the complex, comprehensive effects of climate change on vegetation.

We reviewed the current understanding of vegetation response to drought and elevated CO_2 from leaf to ecosystem scales. In conclusion, plants initiate drought resistance strategies in arid and warm environments, which likely change the carbon flux of forests. Extreme drought massively killing trees is one of the main reasons for forest ecosystem carbon loss. Elevated CO_2 favoring photosynthesis and water use efficiency of plants in a short period of time has been confirmed by a large number of experimental studies, but the effect of CO_2 fertilization is limited by other constraint factors such as light, water and nutrients (N, P). Additionally, on a long-term scale, plants have the possibility of acclimating to warming and elevated CO_2 with a lower net photosynthetic assimilation. The underlying mechanism has not been explained clearly. There is great instability and unpredictability in the physiological mechanisms of vegetation adaptation and mortality under drought [76]. This instability stems from the drought resistance of trees and elevated CO_2 effects on WUE. However, the problem of how far CO_2 fertilization can offset the effects of drought has not been resolved. Whether and to what extent the improved water use efficiency by CO_2 fertilization can withstand drought damage remains unknown.

Understanding the interaction effects of rising CO_2 and drought is crucial for looking forward to future forest ecosystems growing in a drier and warmer atmosphere. Process-based models are important tools for predicting the future interaction of forest ecosystems and atmosphere, however, accurately extrapolating the conclusions derived from individual experiment reports to large-scale ecosystem models requires more comprehensive observational data and process descriptions. There have been studies that provide information that helps improve model simulations, for example, different vegetation type responses to drought [31,33,42] and N, P limitation [53–55,57,58]. Applying that information to model building may help reduce the uncertainty of models. We recommend considering the uncertainties from the following perspectives:

1. Including observational data across different scales. Flux tower measurements, space-time data from large-scale long-term experiments, observation of climate change and vegetation change recorded by remote sensing.
2. Different responses to drought among vegetation types and changing plant species composition of ecosystems over time.
3. Consideration of constraint factors. Restrictions of nutritional elements (N, P), water and light on CO_2 fertilization.
4. Effect of photosynthetic acclimation (down-regulation of photosynthetic capacity).
5. Disturbances. The complexity of the multiple disturbance interactions associated with drought (fires, insects and pathogens).

Overall, a better understanding of mechanisms and scale-up methods are key issues in current research on forest strategies to combat climate change. However, it is worth noting that forests cannot infinitely resist climate change, and the containment of greenhouse gases emissions is the fundamental and necessary way of mitigating global warming and protecting forest ecosystem functions.

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