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REVIEW ARTICLE

Review of drought impacts on carbon cycling in grassland ecosystems

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Abstract Grasslands play a key role in both carbon and water cycles. In semi-arid and arid grassland areas, the frequency and intensity of droughts are increasing. However, the influence of a drought on grassland carbon cycling is still unclear. In this paper, the relationship between drought and grassland carbon cycling is described from the perspective of drought intensity, frequency, duration, and timing. Based on a large amount of literature, we determined that drought is one of the most prominent threats to grassland carbon cycling, although the impacts of different drought conditions are uncertain. The effects of a drought on grassland carbon cycling are more or less altered by drought-induced disturbances, whether individually or in combination. Additionally, a new conceptual model is proposed to better explain the mechanism of droughts on grassland carbon cycling. At present, evaluations of the effects of droughts on grassland carbon cycling are mainly qualitative. A data fusion model is indispensable for evaluating the fate of carbon cycling in a sustainable grassland system facing global change. In the future, multi-source data and models, based on the development of single and multiple disturbance experiments at the ecosystem level, can be utilized to systematically evaluate drought impacts on grassland carbon cycling at different timescales. Furthermore, more advanced models should be developed to address extreme drought events and their consequences on energy, water, and carbon cycling.

Keywords drought, carbon cycling, grasslands, conceptual model, interactive mechanisms, data fusion

1 Introduction

Grasslands account for 40.5% of the earth's land area and approximately 34% of the total carbon in ecosystems (Allaby, 2009; Li et al., 2017). The allocation of sequestered carbon in grasslands, with the dormant ability to store and sequester carbon in soils, remains uncertain (Loiseau et al., 2004; Neely et al., 2009; Harde, 2017). Grasslands exhibit a net source of atmospheric CO_2, as high as 0.5 PG (Scurlock and Hall, 1998; Acharya et al., 2012). Grasslands are affected more easily than other ecological systems (Han et al., 2018; Ingrisch et al., 2018). The increasing frequency and intensity of droughts under the changing climate are impacting both the function and structure of grassland ecosystems (Ali et al., 2017). Under the background of climate change, it is very important to study the response of grasslands to droughts (Sayer et al., 2017).

Climate change may increase the occurrence of extreme disaster events such as droughts (Shrestha et al., 2018). In recent decades, the duration, frequency and intensity of droughts have increased significantly at a global scale (Gidey et al., 2018), especially in semi-arid and arid areas (Cleland and Goodale, 2019). A higher rate of drought risk is projected to occur globally in the future (Huang et al., 2018). At the same time, droughts could radically change the function, structure, and composition of grassland ecosystems (Carlsson et al., 2017; Ochoa Hueso et al., 2018; Stampfli et al., 2018), posing stronger threats to

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ecosystem functioning than that of global shifts and trends in ecosystem regimes (Smith, 2011; Trzcinski et al., 2016; Riis et al., 2017). Droughts are the major cause of inter-annual changes in carbon sinks in grassland ecosystems (Liu et al., 2019). Similarly, the growth rate of abnormal atmospheric CO_2 triggered by frequent droughts has been higher in recent years than in other years (Jiang et al., 2016; Kim et al., 2019). Thus, droughts are intimately linked with terrestrial carbon cycling on a regional to sub-continental scale (Wang et al., 2018). As anthropogenic activities and climate change continue to aggravate droughts, there may be more complicated effects on the carbon cycling of grassland ecosystems (Roy et al., 2016a; Eze et al., 2018; Hao et al., 2018).

Most of the current work reviewing the relationship between carbon cycling and drought has concentrated on forests or terrestrial ecosystems (Anderegg et al., 2015; Lei et al., 2018), while few scholars have scientifically examined and summarized grassland carbon dynamics and droughts (Jia et al., 2018; Li et al., 2018; Yang et al., 2018). Therefore, this paper emphasizes the relations between drought and grassland ecosystem carbon cycling (Lei et al., 2016), which is related to the intensity, frequency, and duration of the drought and its influence upon carbon exchanges among the atmosphere, vegetation, and soil (Green et al., 2019). Furthermore, we propose a novel theoretical framework to address the interaction between environmental factors (drought and other disturbances) and grassland carbon cycling by summarizing previous research.

2 The relationship between drought and grassland carbon cycling

2.1 Overview

Droughts are characterized by a deficiency in precipitation, below multi-year average rainfall conditions, durations of a season or longer, and inability to satisfy the needs of environmental and human activities within one geographic area (Salehnia et al., 2017). The predominant vegetation of grasslands is grass. Grassland examples include Eurasian steppes, prairies, rangelands and savannas (Acharya et al., 2012). In fact, grasslands are different from forests, with the primary process of carbon cycling occurring in the soil (Xiao et al., 2019). In grasslands, soils are immense pools of carbon, exhibiting as much as 89% carbon storage in the form of soil organic matter (SOM). A relatively stable soil environment creates an accumulation of SOM primarily due to the slow turnover of carbon belowground, especially with the capability to augment leaf areas quickly at different conditions (Yuhui et al., 2018; Ganjurjav et al., 2018). Grasslands may be highly susceptible to drought (Ma et al., 2016), which may alter the degree and pattern of carbon cycling under different timescales (from hours to decades) (Fig. 1) (Tardieu et al., 2011). In Fig. 1, productivity represents gross primary productivity (GPP). Carbon pools include vegetation pools, litter pools, and soil carbon pools in the form of soil organic carbon (SOC). Before a drought, stomatal conductance is not strongly limited, and the fluxes of water and carbon are normal

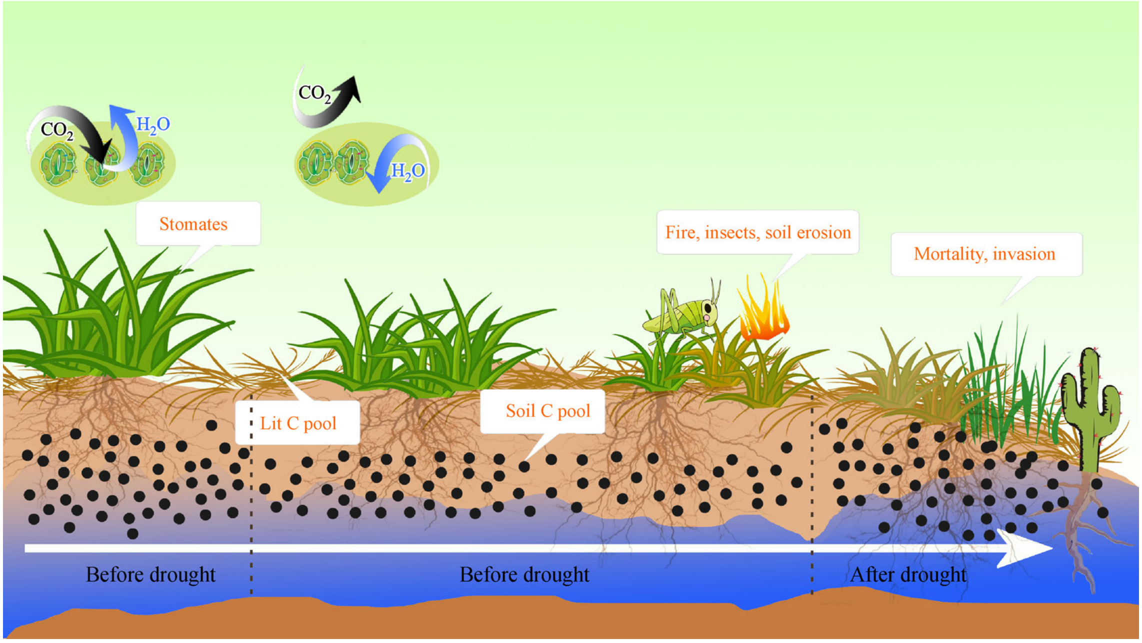

Fig. 1 Schematic of the relation between grassland carbon cycling before, during and after a drought, with the timescales being relevant to the responses and impacts (Modified From Van der Molen et al., 2011).

because soil moisture is high. Drought and high temperatures regulate transpiration via changing stomatal conductance, simultaneously aggravating soil evaporation and lowering soil moisture below the point where water is available for plants, creating a soil drought. During droughts, soil moisture is associated with gradients of drought intensity and duration. As the severity of a drought increases, drought may initiate short and profound impacts on photosynthesis and respiration (Kim et al., 2019). Droughts increase the vulnerability of grassland ecosystems to other disturbances, such as high temperatures, fires, disease, insect infestation, and soil erosion, leading to additional mixed effects on carbon cycling (Tubi and Feitelson, 2019). During or after a drought, ecosystems can also regulate physiologic and structural responses to both buffer and resist the influences of drought. With the intensification of drought, it will become more increasingly difficult to maintain the role of grassland carbon sources and sinks under high spatial and temporal variability and climate variability.

2.2 The impacts of droughts on grassland productivity

Precipitation is a restrictive element for grassland productivity in semi-arid and arid areas (Khalifa et al., 2018). However, during droughts, the change in productivity depends on the physiologic response of plants to obtain available water and the change in vegetation structure. As the intensity and frequency of droughts increase, the water supply for normal plant growth is affected, and plant productivity fluctuates (Chen et al., 2017). Nevertheless, the effects of droughts on grassland productivity are subject to debate. While some studies have found reduced productivity in natural and simulated droughts (Walter et al., 2011; Hoover and Rogers, 2016; Guo et al., 2017; Ingrisch et al., 2018; Stampfli et al., 2018), other studies have found that productivity remained surprisingly stable under local 100-year drought. In contrast, under droughts, higher carbon sequestration in a grassland ecosystem was found in a prairie in Ireland (Jaksic et al., 2006), mixed prairies of North America (Scott et al., 2010), and Brazilian and African savannas (Miranda et al., 1997). Most likely, compensatory growth effects of plants can regulate the distribution of resources between reproductive growth and vegetation (Cuny et al., 2018). With the increase in atmospheric carbon dioxide concentration, water use efficiency is higher in grassland soils than in wet soils (Signarbieux and Feller, 2012; Varga et al., 2017). The responses of GPP to droughts have certain lag effects in the long-term (Reichstein et al., 2013), with the degree of a drought lag effect being controlled by its intensity and duration. Under extreme drought conditions, the two-year fluctuation in grassland productivity has been monitored to determine if it was independent of weather conditions over the following 9 years in tall-grass prairies (Brookshire and Weaver, 2015). In addition, droughts can influence the carbon dynamics of ecosystems after the original response, producing a drought memory in grasses, possibly yielding chaotic responses. Consequently, droughts may even induce multiple equilibrium states in ecosystems (Walter et al., 2011).

Generally, different drought intensities have different impacts on productivity (Lei et al., 2015). In humid regions, minimal drought events can augment plant growth because partly cloudy conditions augment incoming photosynthetically active radiation (Valluru et al., 2016; Dubois et al., 2017), thereby increasing carbon uptake. The rate of community carbon sequestration increases under drought conditions, but regions with less precipitation are more vulnerable to droughts than regions with more precipitation. Conversely, a series of severely extended droughts can significantly reduce grassland net primary productivity (NPP). In fact, aboveground productivity (AGP) may be severely impacted by droughts, but belowground productivity (BGP) is less severely impacted than AGP (Shinoda et al., 2010). Unexpectedly, in a study where the steppe community experienced a severe drought, the AGP and BGP of plants remained stable over the years of drought manipulation in central Europe (Jentsch et al., 2011). Nevertheless, most existing studies focus on the effects of a certain level or intensity of drought, while how ecosystems respond to different levels or intensities of droughts as well as how the evolution of different drought grades affects their productivity have not yet been studied.

However, the duration of droughts and changes in timing of droughts, as well as seasonality, are more likely to generate reduced productivity than enhanced intensity. Drought duration may be the key element influencing carbon uptake and productivity in semi-arid areas (Malone et al., 2016). Aboveground net primary production (ANPP) decreased by 10% with reduced quantity and 13% when timing treatments changed, with the aggregate resulting in a 20% reduction. For Mediterranean grasslands, in comparison to the total precipition, the variety in rainfall timing had a greater impact on GPP. Additionally, droughts decreased gross primary productivity (GPP) at a 110-day cycle but had no obvious effect on GPP in August. Therefore, predicting the ecosystem response to droughts should consider not only drought severity but also drought duration under climate change. The tolerance of soil microbes to droughts in semi-arid agro-ecosystems is strongly influenced by previous land use. Thus, Mediterranean grassland ecosystems are sensitive to long-term droughts. As the duration of a drought increases, the ecosystem nitrogen dioxide flux decreases, even though nitrogen weakens the impact (Nogueira et al., 2019). In addition, the phase of plant development may influence the drought response (Heschel and Riginos, 2005) with saplings being highly vulnerable to drought events (Williams and Holland, 2007). Similarly, the seasonality of droughts may dominate the degree of carbon uptake and carbon cycling. A change in Northern Hemisphere spring droughts influences the function and structure of ecosystems more than a Northern Hemisphere fall or summer droughts for the northern prairie of the US (Heitschmidt and Haferkamp, 2003; Heitschmidt and Vermeire, 2006). Therefore, various intensities and timings of droughts produce different effects on grassland carbon cycling.

Droughts also have a serious impact on land productivity. Droughts can reduce the total primary productivity of terrestrial ecosystems by inhibiting photosynthesis. It can also reduce autotrophic and heterotrophic respiration of ecosystems. At the same time, droughts can indirectly influence the productivity of terrestrial ecosystems by affecting other forms of interference, such as augmenting the intensity and frequency of fire, increasing plant death rates, and increasing the occurrence of disease and insect infestations, as shown in Fig. 2.

Different grassland ecosystems have different responses to droughts. The magnitude of drought effects depends on the drought sensitivity and the ripeness of grass. For example, C3 species may be more drought-sensitive than native C4 perennials because of their different water efficiencies (Roby et al., 2017b). Generally, varieties of high botanical species boost stable carbon storage of aboveground vegetation during droughts (Bloor and Bardgett, 2012). Moreover, in comparison to dominant species, less dominant species were more vulnerable to drought impacts (Caracciolo et al., 2016). Furthermore, some inferior adaptable species cannot rebound to pre-drought conditions (Hofer et al., 2016).

However, the impact of droughts on the carbon allocation in grasslands is still unclear, particularly with regard to soil carbon. In general, droughts may result in an increase in carbon allocation for roots and soils that can be transferred into more stable root systems and soil carbon pools (Mirzaei et al., 2008), despite different intensities and durations of droughts (Karlowsky et al., 2018). Drought intensity partially influences the fate of carbon distribution for photosynthetic products (Jentsch et al., 2011). Extreme drought limits carbon translocation from aboveground to belowground composition, but moderate drought results in carbon assignment to the organs most urgently demanding carbon under high water stress (Wang et al., 2018a). In dry climates, plants may search for water to better distribute it to deep roots (Battistiet and Sentelhas, 2017). The long-term consequences and the impacts of droughts on the overall importance of carbon and soil carbon reservoirs need further investigation. In contrast, some studies have indicated that droughts may reduce the flow of carbon from grass roots to soil pools (Suseela et al., 2012). Presumably, droughts reduce carbon sequestration and increases the retention time of newly assimilated carbon in leaf biomass, thus prolonging the time interval of carbon distribution from plants to soil (Peng et al., 2017). In biogeochemical models of long-term carbon budgets for ecosystems, the concept that drought reduces the amount and rate of carbon transferred from plants to soils needs to be considered (Yuste et al., 2011).

2.3 The impacts of droughts on soil respiration

Soil respiration (heterotrophic respiration) litter and the decomposition of soil organic matter (SOM) and autotrophic respiration (mycorrhizal and root respiration) may account for up to 70% of total ecosystem respiration (TER) (Van der Molen et al., 2011), which is tightly linked to GPP on an annual timescale (Suseela et al., 2012; Wang et al., 2015), and soil respiration is the major route of carbon flow from grasslands to the air. This transfer plays a key role in understanding the impacts of regional climate change and provides one of the largest total fluxes in carbon cycling (Ford et al., 2012; Urbanek and Doerr, 2017). Thus, soil respiration is a key ecological feedback mechanism for climate change, and it has become the core research topic related to global carbon cycling (Canarini, et al., 2017).

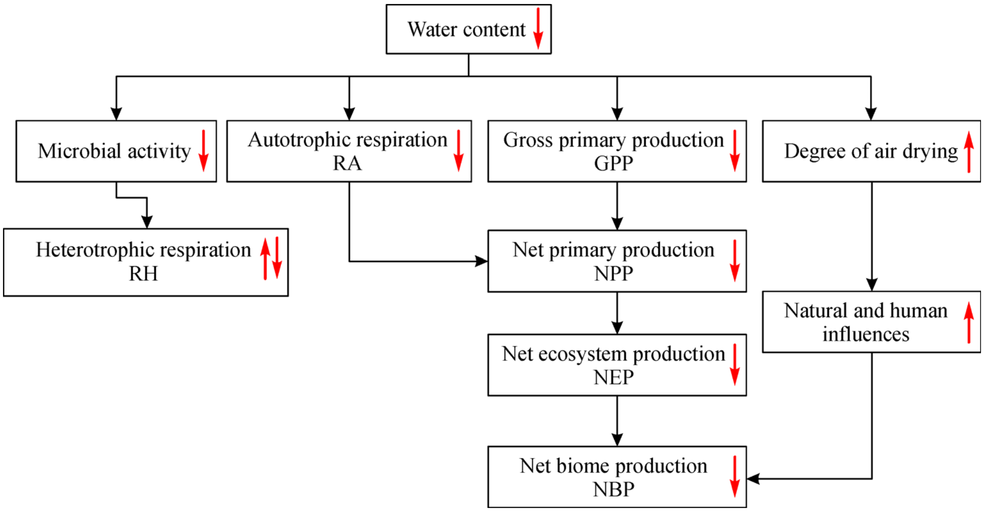

Fig. 2 Drought impacts on terrestrial ecosystem productivity (Note: "↑" and "↓" represent increases and decreases, respectively).

Soil respiration is determined by the complex interaction of biology and biological factors, including photosynthesis, microbial action, soil moisture, extracellular enzymes, SOC, soil temperature, rainfall and soil depth (Zhong et al., 2016; Kukumägi et al., 2017). Substantial evidence shows that soil temperature, soil moisture and GPP are three primary drivers of soil respiration (Joos et al., 2010; Thiessen et al., 2013). Soil temperature affects the organic decomposition process and material transport by affecting soil activity and microbes, and soil temperature also influences the processes of photosynthesis and respiration by affecting the substrate supply of physiologic and metabolic activities of plants (Kim et al., 2019). Soil moisture affects the vegetation root system and soil microbial respiration by affecting soil O_2 diffusion and affects metabolic substrate by affecting respiration, thus controlling vegetation photosynthesis. On the one hand, GPP affects net ecosystem exchange (NEE) by controlling the photosynthetic intensity of vegetation, and on the other hand, GPP affects respiration. Substrate supply has an impact on ecosystem respiration, as shown in Fig. 3.

Droughts can alter the relation between soil respiration and driving factors, especially temperature sensitivity. When the soil-water deficit becomes a stress factor, it may replace temperature as the key controlling factor of soil respiration (Falloon et al., 2011). The interconnection of soil respiration and temperature can be impacted by droughts because droughts reduce the dispersion of extracellular enzymes and the soluble carbon stroma (Liu et al., 2018). During drought seasons, soil respiration rates are more limited by moisture than temperature (Wang et al., 2014). Consequently, soil moisture plays a key role in affecting soil respiration in complex ways both directly and indirectly (Wang et al., 2014). The direct impacts of soil moisture on soil respiration have been documented in many studies (Mishra and Singh, 2011; Wang et al., 2014). In contrast, indirect effects occur with physical changes in the soil environment that affect pervasion rates and delays in biological processes, such as changes in the mode of supplying microbial respiration substrates (Daly et al., 2008; Manzoni et al., 2014). The effectiveness of a matrix relies heavily on soil moisture; thus, this scenario can explain why droughts dampen the increase in soil respiration with increased temperatures (Andresen et al., 2018).

Environmental factors such as droughts alter soil respiration rates. Some studies have reported a surprisingly low impact of droughts on soil carbon content (Kallenbach et al., 2019). Soil can buffer short-term extremes on the soil surface (Niboyet et al., 2017). Ultimately, microbial-mediated decomposition of SOM mainly contributes to the CO_2 flux in soil, which is the most prevalent origin of CO_2 originating from terrestrial ecosystems (Yuste et al., 2011). The role of microbial populations in the decomposition of SOM in response to drought events of different durations and intensities may be critical (Wang et al., 2014). Droughts not only limit physiologic performance and the pervasion of microbes and nutrients to soil pore space microbes, but also expose microflora to a significant adaptive process. As soil further dries, microbial community composition may be controlled by drought-tolerant species (Manzoni et al., 2012). Additionally, severe drought dramatically decreases microorganism performance and decreases mycorrhization and cellulose decomposition rates (Jentsch et al., 2011), especially in close relation to the composition of litter (Bloor and Bardgett, 2012; Sanaullah et al., 2012).

Other studies have reported increased soil-CO_2 emissions during drought. Similarly, high temperatures following droughts have been documented to enhance ecosystem respiration (Zhao and Running, 2010). Nonetheless, droughts may result in an abnormal accumulation of SOM. As decomposition rates decrease, the unstable carbon content in the form of aging biomass increases, which is related to the death of leaves and roots caused by drought (Scott et al., 2009; Martí-Roura et al., 2011). Thus, litter decomposition provides fungi for microbial activities and releases CO_2 into the atmosphere. Rainfall after droughts may strongly stimulate soil respiration owing to more favorable conditions for microbial activity. Subse-

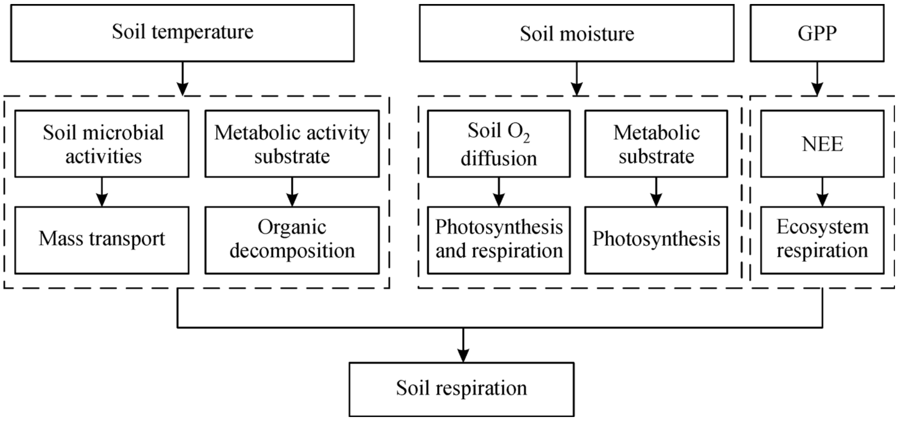

Fig. 3 The effects of GPP, soil temperature, and soil moisture on soil respiration.

quently, soil microorganisms respond to larger respiratory bursts in most cases, excluding soil that has experienced extreme drought-stress periods (Ebrahimi et al., 2019). Despite the large bursts of CO_2 efflux induced by rewetting after prolonged droughts, soil-CO_2 emissions can still be reduced by 26% (Joos et al., 2010). Surprisingly, in one study, root respiration did not increase after prolonged drought despite increasing soil temperatures (Luo and Zhou, 2010). Because litter quantity during drought is not expected to decline due to reduced decomposition, carbon inputs (e.g., root exudates) into the soil are more likely affected (Christel et al., 2013). Furthermore, soil respiration originates from deep soil layers with different temperature and humidity patterns. Recent research suggests that the respiratory effects of a young carbon stroma can be less affected by droughts than that of an older carbon stroma in the ground litter of grassland ecosystems (Andresen et al., 2018). In fact, an extended severe drought may potentially mobilize large amounts of carbon, the so-called 'microbial priming effect' (Thiessen et al., 2013; Perveen et al., 2014). Therefore, soil microbial consumption could be the major factor of increases in respiration.

The impact of droughts on soil respiration has not only an immediate effect but also certain carry-over effects, which are characterized by the frequency, timing, and intensity of droughts (Wang et al., 2014). Carry-over impacts largely depend on the composition and size of the soil carbon pool and drought intensity and its duration (Dulamsuren et al., 2019). After a drought, carbon pools in volatile soils generally reach a new equilibrium quickly. On the one hand, it will take longer for stable pools to reach a new counterpoise. On the other hand, the nitrogen mineralization and delayed decomposition could be favorable for vegetation growth (Dulamsuren et al., 2019). Moreover, the intensity and duration of drought, soil characteristics, and precipitation quality can affect soil moisture recruitment (Knapp et al., 2008). In addition, soil respiration has different responses to different intensities of droughts. Droughts, especially extreme droughts, can affect soil respiration for periods from one to nine years (Wang et al., 2014). However, these extreme pulses of soil respiration are not well described by present patterns, and deviations are introduced in calculating respiration, relying on drought intensity and frequencies. Furthermore, in comparison to drought intensity, the timing of droughts has a larger effect on soil respiration. On a grassland in North America, when precipitation decreased by 30%, the average seasonal respiration of the soil decreased by 8%; when precipitation duration decreased by 50%, the soil respiration decreased by 13% (Zhou et al., 2006); and the increase in drought interval was accompanied by an increase in rainfall intensity, which increased by 20% when both occurred simultaneously (Harper et al., 2005). Long-term drought could also influence the respiration of soil, SOC dynamics, and underground microbial processes by altering community composition, especially the presence of leguminous species. Drought remnants can also adjust the soil respiration rate by changing abiotic driving factors and microbial community structure to adapt to re-wetting events in ecosystems (Evans and Wallenstein, 2012). However, the role of plant diversity in regulating soil respiration in response to droughts remains unclear. Overall, high productivity and high plant diversity may offset the effects of droughts to some extent (Nogueira et al., 2017). The decrease in organic nitrogen concentrations in different plant communities may also have adverse impacts on soil respiration (Dias and Brüggemann, 2010). Additionally, the distribution of species in soil also affects the quality of the litter, the soil biota composition, and the SOM turnover rate (Li et al., 2014). Thus, the effects of plant community diversity on soil respiration need to be further studied (Waldrop et al., 2017). The activity and structure of the soil biotic community are strongly influenced by the constitution of the plant community (Kardol et al., 2010). Therefore, the degree of change in soil respiration depends on substrate supply, community composition, species richness, and the frequency (duration), timing, and intensity of a drought.

2.4 Complex effects of droughts and other disturbances on carbon cycling

Disturbances are not independent of each other and may create unfavorable conditions for other disturbances, such as high temperature, fire, insects, invasion and soil erosion (Jia et al., 2017). Droughts also reduce plant resistance to damaging disturbances, such as pests or other disturbances (Van der Molen et al., 2011).

However, droughts and higher temperatures are likely to be experienced synchronously (Mueller and Seneviratne, 2012; Eagle et al., 2013). Perhaps grassland ecosystems can physiologically recover from a single stress, but it is difficult for them to recover from a combination of both drought and heat stress than either individually (Roy et al., 2016), leading to more dramatic reductions in the canopy photosynthetic rate, leaf photochemical efficiency, and root dry weight (Li et al., 2016). Both the singular and mutual effects of droughts and temperature on the carbon cycling of grasslands are indistinguishable (Hoover et al., 2017). Higher temperatures can aggravate the impact of droughts, and if these higher temperatures occur during a growing season, grassland can be an extremely harsh environment (Louhaichi and Tastad, 2010). Additionally, the effects of droughts on plants can lead to carbon losses in ecosystems by increasing respiration and/or reducing productivity (Van der Molen et al., 2011). The old carbon in deep soil may be protected by microbiological degradation due to a lack of a lightly degradable matrix, but grassland ecosystem soil carbon storage is susceptible to climate change (Su et al., 2017). The increased drought degree and frequency in the Northern Hemisphere summer will reduce

NPP, soil organic matter supply, and decomposition rate (Amézquita et al., 2010). Presumably, soil humidity and temperature reduced soil carbon storage and accelerated decomposition from 2002 to 2007, thus releasing more carbon (Amézquita et al., 2010).

Do widespread droughts have profound effects on the impacts of wildfires and vegetation dynamics? Surprisingly, in a study, a drought had a minimal effect on fire in the Tuer River Basin of Mongolia (Saladyga et al., 2013). On the central plains of North America during drought periods, forbs and erosion have increased, grass productivity has decreased, and fuel restriction has decreased the impact of fires. In wet decades, with the stabilization of soil and the abundance of fuel, the yields of grass increased (Jeong et al., 2015), and droughts caused the frequency and intensity of wildfires to increase (Reichstein et al., 2013). Ecosystems affected by droughts have a higher fire risk due to dry vegetation and litter acceleration, where combustion occurs more easily (Astiani et al., 2018). However, the combination of fires and droughts diminishes aboveground live carbon, suggesting that plants cannot survive under these two stresses (Peck et al., 2017). The influence of droughts can produce transient carbon pulses much larger than those of fire (Scott et al., 2009). Fires and droughts can increase short-term soil organic carbon accumulation, but their long-term impacts on carbon cycling are still unclear. Fires and droughts increase the short-term accumulation of SOC, but the singular impact of a drought remains unclear.

In addition, droughts have had significant impact on diseases and insects, with substantial effects on tissue dieback in plant communities exposed to a 100-year drought in grasslands. During a drought period, insects caused root death, plant destruction and community composition changes (Coupe, et al., 2009). Similarly, *Cordyceps* populations may also increase after a drought. In many places, drought has spawned grasshopper flocks, further destroying the vegetation (Peck et al., 2017). The causes may be density-independent consequences of abiotic conditions, the improved flavour of water-stressed plants or decreased populations of natural enemies (Thomson et al., 2010). These scenarios may interact with each other and are not exclusive (Padgham et al., 2015).

Presumably, not all droughts are so fatal that they could push a system beyond the threshold of dynamic equilibrium, creating a novel system trajectory. Many biological communities have a specific inertia for the transformation of species composition and can maintain natural adaptation over more rivalrous communities (Jentsch et al., 2011). Only less-severe drought events may convert competitive interactions among plants and change successional pathways by reducing the inertia of a given system (Wang et al., 2018b). Long-term droughts can also lead to plant death, especially for high-yielding forages (Valliere et al., 2017). However, drought seasonality is important for preventing vegetation mortality. For instance, extreme Northern Hemisphere summer droughts reduce the abundance and diversity of micro-structural plants by killing perennial Gramineae plants, while extreme Northern Hemisphere winter droughts do not influence perennial plants and have little impact on soil microflora (Whitford and Steinberger, 2012). A Northern Hemisphere spring drought has the potential to endanger C3 plant communities, whereas a Northern Hemisphere summer drought would be detrimental to C4 plants (Scasta et al., 2016; Aseeva et al., 2018).

Droughts may also be important triggers for biological encroachment. The severity and duration of droughts determine the success rates of invasive species (Van der Molen et al., 2011). To some extent, grass mortality may also facilitate invasion though alien plants (Diez et al., 2012). As a consequence, extended droughts can shift species compositions toward shorter-growing, less-productive, or more drought-tolerant species (Fauset et al., 2012).

Invasion also depends on the availability of resources, and persistent drought may be beneficial to preventing intrusions. In the early stages of a drought, upper soil moisture is used by grassland species, thus impeding the establishment of bare herbs or shrub seedlings (Schrama and Bardgett, 2016). Thus, recurrent droughts restrain the invasion of plant communities and, consequently, increase community stability (Jentsch et al., 2011).

Soil erosion is an important factor determining the carbon content in soil (Thorpe, 2011). A decline in vegetation cover plays a key role in accelerating soil erosion and runoff, reducing resistance to droughts and increasing the degradation severity and degree of droughts (Conant, 2010). Soil erosion was the most severe effect of the catastrophic Dust Bowl drought that occurred in North America in the 1930s (Grimstead et al., 2016). However, grassland ecosystems have certain buffering capacities that allow them to withstand droughts in one season. Nevertheless, droughts spanning two or more seasons can decrease vegetation cover remarkably (Tollerud et al., 2018). Accordingly, prolonged droughts can trigger an immediate loss of biomass due to a reduction in grasses and forbs, resulting in large areas of bare ground (Longo et al., 2018). Therefore, regime shifts may have profound effects on ecological services.

2.5 Net effect of drought on the carbon cycle of grassland ecosystems

With increased spatio-temporal changes and climate variability influenced by climate change, the ability of grasslands to serve as carbon sinks will become increasingly difficult to maintain (Xu et al., 2018). Droughts may also have negative impacts on ecosystem functions that are not commensurate with their short-term durations (Huang et al., 2017). Recently, carbon sequestration in ecosystems accumulated over several years has been eliminated by severe long-term droughts (He et al., 2018). In a struggle for ‘food’ resources, microbes must constantly eat ‘old’ soil carbon (Thiessen et al., 2013). Therefore, drought is a key impact factor in the grassland ecosystem carbon cycle. Droughts have a negative effect on soil carbon storage due to its influence on local soil organic matter (SOM) initiation caused by plant litter (Sanaullah et al., 2014). Inversely, droughts have adverse impacts on water holding capacity, SOM content and soil diversity (van Eekeren et al., 2008). Moreover, enhanced soil carbon sinks can reduce drought risks (Conant, 2010), making grasslands strongly regenerative and able to quickly rebound from frequent damage such as that from droughts and grazing (Neely et al., 2009). However, whether the carbon sink function of grassland ecosystems can change has not yet been explicitly determined, relying heavily on the soil base of grasslands and drought conditions.

The carbon source/sink function of grassland ecosystems is highly uncertain under different drought scenarios. Ecosystem carbon dioxide swapping (NEP or NEE) is an indicator that can be used to measure the response of ecosystem levels to climate change (Baldocchi, 2011). Whether droughts have suppressive applications for increasing carbon accumulation depends on the relative magnitude of GPP decreases and total ecosystem respiration (TER) (He et al., 2018). The efficiency of water use and net carbon assimilation capacity increase following a drought without changes in respiration, thereby promoting a net carbon uptake into a system (Mirzaei et al., 2008; Scott et al., 2010; Baldocchi, 2011; Hussain et al., 2011; Signarbieux and Feller, 2012). By contrast, a severe drought affects GPP more than TER, causing deterioration of NEE (Sponseller, 2007; Jongen et al., 2011; He et al., 2018). Surprisingly, ecosystems on some prairies are essentially carbon neutral after droughts. In addition, droughts may have a certain delayed effect on NEE. Drought frequency, soil properties and changes in precipitation influence ground humidity. The delayed impact of partial soil water replenishment has been documented to last for two years and result in up to 40% of the direct NEE anomalies (Van der Molen et al., 2011).

Overall, in comparison to drought intensity and duration, drought duration and seasonality could result in a greater effect on NEE. Grassland ecosystems can endure moderate drought conditions and maintain normal ecosystem functions. NEE also significantly increases along a gradient of declining drought intensity (Han et al., 2018). The extent of change in NEE seems to depend not only on the severity and duration of droughts but also on their timing, especially in relation to the growth stage of grassland vegetation (Balogh et al., 2015). For Mediterranean grasslands, in comparison to rainfall total, the timing of rain events has more significant impacts on NEE (Nogueira et al., 2018). On a yearly basis, ecosystems are a water purification pool and carbon source, depending on Northern Hemisphere winter precipitation and the important short-term Northern Hemisphere spring, which indirectly indicates the importance of drought duration. Moreover, changes in seasonal patterns of rainfall will have direct impacts on the carbon dynamics of ecosystems, key factors determining carbon sequestration and emissions in grasslands (Kwon et al., 2008). Indeed, Northern Hemisphere summer droughts result in increased carbon losses, whereas an extreme drought in the cool season leads to decreasing Northern Hemisphere spring carbon absorption (Scott et al., 2009). In addition, NEE in different grassland ecosystems has different responses to drought intensity. The impact of extreme droughts on CO_2 efflux is very marked, sequentially decreasing in different temperate grassland ecosystems such as meadow, *Leymus chinensis* and *Stipa grandis* grasslands (Song et al., 2016). Interestingly, droughts have resulted in carbon sources in grassland ecosystems; however, droughts have enhanced carbon sinks in shrubland ecosystems (Chen et al., 2012).

Ecosystems that suffer from droughts can rapidly switch from servings as carbon sinks to carbon sources. Hence, there are magnitude thresholds that cause grasslands change (Zhang et al., 2015). Here, the increase in NEE because of drought-like exceptions, the intensity of a drought does not surpass the adaptive ability of the ecosystem despite the events occurring has represented extreme local conditions for 100 years (Mirzaei et al., 2008). Generally, the physiologic threshold of a drought is below 0.4 in terms of relative extractable water, leading to both GPP and transpiration decreasing as a result of stomatal closure. Moreover, moderate droughts may cause an acclimated increase in stomatal density and net CO_2 assimilation rate, but severe droughts may reduce both factors (Han et al., 2018). Furthermore, some study results have shown that when the total rainfall over three months is 75 mm and the evaporation/rainfall ratio over these three months is 0.15, the critical threshold for survival is reached and below which death begins (Tessema et al., 2016). However, the thresholds of shifting ecosystem functions are unclear and may be associated with the intensity and duration of a drought and ecosystem structure.

3 A conceptual model of interactive mechanisms between droughts and grassland ecosystems

Generally, patterns of vegetation water use can be dramatically altered by droughts (Tang et al., 2018). Nevertheless, a reduction in photochemical efficiency and photosynthesis may cause a loss in productivity under more severe drought conditions (Gao et al., 2017). It is possible that grasslands can change from serving as carbon sinks to serving as carbon sources under great environmental stress exceeding the threshold of the ecosystem, so thresholds or turning points of shifting ecosystem functions must exist. However, how drought affects ecosystem functioning is poorly understood. Overall, we should focus on investigating the interactive effects among grassland carbon cycling and disturbances, particularly at the ecosystem level. Thus, understanding how droughts influence vegetation water use is important to managing carbon cycling. However, the interactive mechanisms between droughts and carbon cycling have not yet been completely understood, especially at an ecosystem level. Furthermore, by summarizing previous research, we propose a novel theoretical framework to address the interaction between environmental factors (droughts and other disturbances) and grassland carbon cycling.

In the proposed theoretical framework, the following hypothesis is given: the mechanisms of carbon cycling are related to the intensity and duration of droughts, other disturbances and ecological adaptability (Fig. 4). The X-axis and Y-axis represent the duration and intensity of the drought, respectively; the Z-axis represents the carbon flux ($gC/(m^2 \cdot a)$). The hyaline space plan shows the ecosystem scale interpretation. Next, the green and red curves in space separately express GPP and TER, respectively, and the light green and red shaded areas reveal the size of the carbon sink and source, respectively; the crossing point is the turning threshold of the carbon sink/source. The blue and red boundaries display hydraulic fracturing and the beginning of carbon deficiency, respectively. Lastly, the cylinder is indicative of other disturbances magnifying or counteracting the effects of drought, resulting in more serious consequences such as species mortality and invasion.

First, hydraulic failure is defined as occurring when the degree of drought is adequate to force plants to surpass their criticality values such that the critical evapotranspiration rates exceed irreversible desiccation, especially under high temperatures (Larionov et al., 2016). Hydraulic failure predicts that decreased supernal evaporative requirements and soil water content result in lower stomatal conductance, preventing water loss and plant tissue desiccation, with complete desiccation inducing cellular death. When hydraulic failure further deteriorates, it may eventually lead to the destruction of vegetation, in turn affecting the processes of carbon cycling, such as the transportation of new carbohydrates (McDowell et al., 2008). If the intensity and duration of drought are long enough that plants deplete water before releasing carbon, then the possibility of hydraulic exhaustion is greater. Soil hydraulic conductivity is a function of texture, water content, hydraulic conductivity and depth to groundwater (Franks et al., 2007).

Second, carbon starvation is defined as a shut spiracle to avoid hydraulic fracturing, causing a decrease in photosynthesis and carbon sequestration, whereby the plant starves due to the continual metabolism demand for

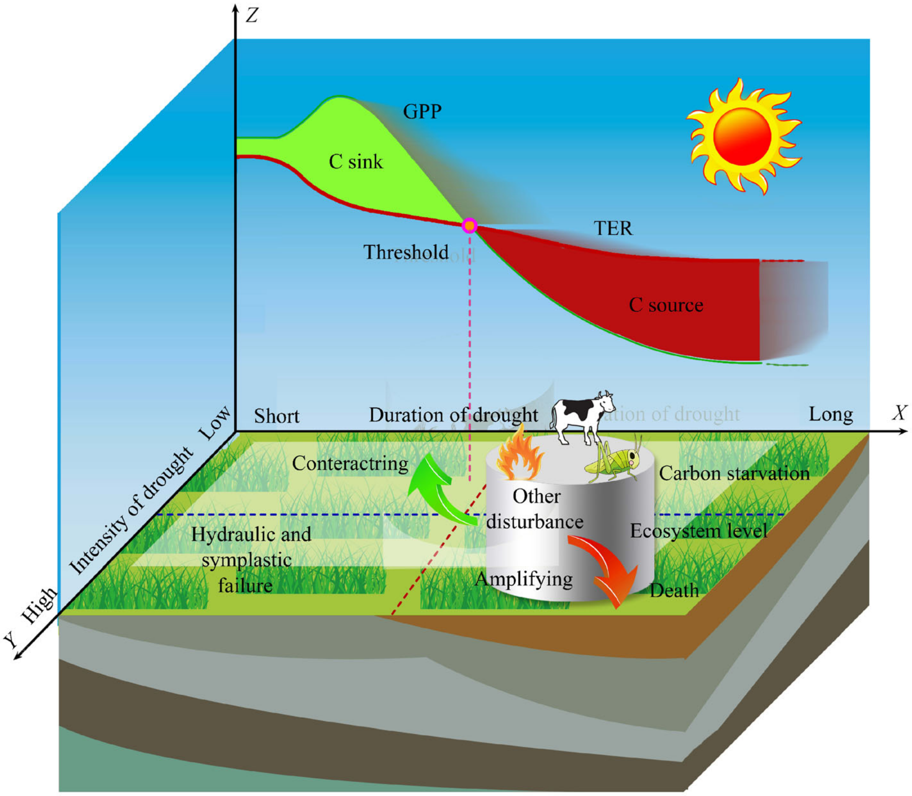

Fig. 4 Schematic of interactive mechanisms between droughts and grassland ecosystems.

carbohydrates, which is further deteriorated by photoinhibition or incremental respiration and high temperature in drought (Trifilò et al., 2017). Therefore, carbon starvation can be driven by both hydraulic and non-hydraulic mechanisms. If a drought is not severe enough or does not last long enough to trigger hydraulic failure, then carbon starvation is highly likely, but if a drought lasts long enough, then the duration of starvation may exceed the equivalent amount of carbon stored by plants. Moderate droughts can reduce growth and increase defensive carbon allocation, but severe or persistent droughts can decrease the formation of defense compounds (Thomey et al., 2014). The duration of a drought is important because stored carbohydrates temporarily buffer the effects of carbon allocation. In addition, drought timing (seasonality) is a crucial contributor to hydraulic failure and carbon starvation because the effects of droughts occurring at different growth stages of vegetation vary significantly. Additionally, according to the definition of carbon starvation, the transformational thresholds of carbon sinks/sources may occur before an ecosystem suffers from it.

Third, other disturbances, such as heat waves, fires, diseases and insects, biological invasion, and soil erosion, may interact with droughts. The changes in the climate system induced by droughts can be magnified or counteracted by the frequency and intensity of other disturbances (Vargas and Paneque, 2019), indirectly aggravating or reducing carbon starvation and hydraulic failure. To some extent, the impacts of other disturbances can be amplified by droughts. Similarly, drought occurrence may facilitate or restrain biotic and abiotic attack via changes in existing circumstances. These effects can aggravate or mitigate the hydraulic failure or carbon starvation induced by droughts. For example, the CO_2 fertilization effects in grasslands depend upon differences in the seasonal effects of rainfall. In addition, two recent studies demonstrate that as the climate becomes drier and warmer, the CO_2 fertilization effect will diminish or even disappear (Nowak, 2017; Obermeier et al., 2017). Therefore, future increases in drought intensity and duration will increase mortality through water depletion or carbon starvation and more seriously affect water and carbon cycling.

Moreover, ecosystems show certain resistance and resilience to be able to buffer the effects of droughts. Grassland ecosystems can adapt to moderate droughts and maintain normal ecological functions. In particular, grassland soils have relatively low sensitivity to droughts, mainly due to the contribution of a large concentration of soil carbon, and can buffer short-term extreme events superficially. Surprisingly, grasses under drought conditions retain long-term stress signatures that help them respond more quickly and protectively to repeated droughts (Zwicke et al., 2013). The adaptation strategy of plant-soil interactions plays an important role in the short term stability of carbon cycling under extreme drought conditions. At the species level, therefore, an individual might not be responsive to droughts, but an ecosystem can significantly respond (Weißhuhn et al., 2011). At the ecosystem level, grasslands may show strong and rapid structural and functional responses to droughts, and the response of plants to drought has inherent hysteresis (Bloor and Bardgett, 2012; Craine et al., 2013; Yang et al. 2018). Drought can result in wholesale restructuring of grassland ecosystems because they surpass the ecological thresholds of dominant or keystone species, whereas other changes may be buffered due to the compensatory dynamics of some species (Smith, 2011; Kim et al., 2019). Primary response dynamics to droughts involve theoretical critical points and thresholds of regime shifts, subsequent rapid changes in energy flow, nutrient circulation and gas exchanges, and species-specific responses in terms of primary productivity are slow and sluggishness in productivity, plant-soil interactions, microbial priming effects and mortality (Jentsch et al., 2011).

Eventually, droughts can change the structure and function of ecosystems, altering water and carbon flows. These mechanisms, including these four aspects, may operate either individually or in combination to enhance interactions between droughts and grassland carbon cycling. However, it is not clear whether the intensity and duration of droughts can trigger the evolution of the interaction process between drought and grassland carbon cycling. Additionally, determining what response occurs, first at the molecular level and then at the ecosystem level, or both simultaneously requires more research. At the same time, grassland ecosystem models could explain some processes to quantify biogeochemical responses to arid conditions (Kipling et al., 2016; Wagena et al., 2016; Sándor et al., 2017). However, the limitations in modeling responses under drought conditions become especially apparent when a plant's ability to adapt is greatly exceeded (Zaka et al., 2016 and 2017). This aspect is a strong limitation in several state-of-the-art biogeochemical models. Further research must be conducted to determine the adaptation process at the molecular, ecological and biochemical levels and link this process to functional parameters. To better understand how plants respond to climate change, long-term adaptation mechanisms need to be studied carefully, and projections and recommendations need to be developed to adapt to droughts (Signarbieux and Feller, 2012).

4 Discussion and conclusions

We reviewed how droughts have affected carbon cycling in grassland ecosystems over several decades in arid and semi-arid areas and found droughts to be the main natural factor threatening the carbon cycling of grasslands. We proposed a novel theoretical framework to address the interaction between environmental factors (droughts and other disturbances) and grassland carbon cycling. With global climate change, droughts have become more frequent. However, in areas where human activities are intense, humans are no longer merely affected but actively influence and even change the development process of droughts (Liu et al., 2019; Nogueira et al., 2019). Under intense droughts with longer durations and higher frequencies and with ecosystems characterized by stress, thresholds are not synchronized and are expected to more strongly influence carbon cycling. As a result, the frequency (duration), timing, and intensity of droughts have different influences on grassland carbon cycling. There is still many uncertainties regarding the effects of droughts during and after droughts ranging from months to years. However, the other interferences caused by droughts can magnify or offset the effects of droughts on grassland carbon cycling, creating comprehensive effects.

Unfortunately, the present understanding is limited given the exiguous and dispersive field data and coarse models. In addition, ecological disturbances, such as droughts and other disturbances, suffer severely from a lack of systematic observations at the ecosystem level (Van der Molen et al., 2011). At present, the inter-annual variations in carbon fluxes only reflect short-term (from hours to months) responses of grassland carbon cycling to droughts but cannot be expected to apply over longer timescales (from months to years). We need multi-source data and models to systematically assess the effects of droughts on grassland carbon cycling from hours to years, including developing single and multi-disturbance experiments at the ecosystem level (Lei et al., 2016). Furthermore, more advanced models should be developed to address extreme events and the consequences of droughts on energy, water, and carbon cycling.

In conclusion, we can advance our understanding of the impacts of droughts on grassland carbon cycling in response to drought and grassland carbon cycling processes. We recognized the main gaps among correlated processes, observations and current model formulations. Thus, we propose the following future development direction:

The functional relations among the frequency (duration), timing, and intensity of droughts and different fluxes (GPP, soil respiration and NEE) are not sufficiently advanced; the short- and long-term impacts on ecosystems affected by droughts and their implications on GPP, soil respiration, and NEE are not well represented in most experiments and models at the ecosystem scale. In future studies, we should explore and determine the frequency of drought duration, intensity, and GPP; the interaction relationship between soil respiration and NEE; and the response mechanism of grassland ecosystem response to drought. Furthermore, the functional relations between the intensity, duration, and timing of droughts and different disturbances (heat waves, fires, insects, diseases, invasion, and soil erosion) are still not adequately established and quantitatively forecasted. Therefore, further study should include the responses of grassland carbon fluxes to different disturbances under varying intensity, duration, and timing of drought scenarios to identify the control factors of grassland ecosystem functions based on the same spatial-timescale, and the current models should take the interactive mechanisms between droughts and different disturbances into account to assess their combined influence on grassland carbon cycling.

At the same time, there are thresholds or turning points that can lead to a change in grasslands from a sink to a source; however, the precise functional relations between drought characteristics (frequency, duration, timing, and intensity) and carbon-function thresholds are poorly known and should be further studied. Because the effect of droughts on soil carbon pools in grasslands is highly uncertain, we should use quantitative methods to determine the relation between soil carbon and drought frequency (duration), timing, and intensity in the context of global change. Models should also be developed to simulate the decomposition rates of soil carbon under global climate change and drought stress. It is largely unknown how ecosystems adapt during or after droughts and how species interactions and competition change ecosystem functions, such as carbon fixation and turnover rate, in different grasslands. It is necessary to integrate multiple types of data to quantify the impacts of droughts on carbon cycling; thus, systematic observations and modeling of ecological system level need to be carried out.

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