



Plant growth and mortality under climatic extremes: An overview



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ABSTRACT

Ongoing climate change has caused extreme climatic events to happen more frequently, which can fundamentally threaten plant growth and survivorship. In this review paper, we found that extreme climatic events, such as heat waves, frost, drought and flooding, usually reduces plant production and induces mortality. The magnitude of impacts on production and mortality are exceedingly variable, which likely result from different severities of the climate extremes, sensitivities of various processes, vegetation types, and inherent regulatory mechanisms of plants and ecosystems. Climatologically severe events may not necessarily trigger plant responses. Different processes respond to the same extreme events differently. Such different responses also vary with species. Moreover, plants likely activate a variety of physiological and molecular mechanisms regulate their responses to extremes. Documenting those variable responses and identifying their causes are critical to advancing our understanding. Nevertheless, our research has to move beyond the documentation of phenomenon to reveal fundamental mechanisms underlying plant responses to climate extremes. Toward that goal, we need to define extreme climatic events under a plant perspective and evaluate different response patterns of various processes to climate extremes. In this review, we also propose to focus our future research on manipulative field experiments and coordinated networks of experiments at multiple sites over different regions to understand the real-world responses of plants and ecosystems.

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1. Introduction

Ongoing climate change has resulted in increases in climate extremes, such as droughts, heat waves, heavy rainfall, and frosts (IPCC, 2007). Climate models predict more extreme climate in a future world with increases in extreme high temperatures, decreases in extreme low temperatures, and increases in intense precipitation events and drought (Easterling et al., 2000; Orłowski and Seneviratne, 2012). For example, the intensity of precipitation events is projected to increase over most regions of the world regardless of increases or decreases of total annual precipitation (Tebaldi et al., 2006). Under global warming, enhanced variability in temperature results in more frequent, persistent, and intense

heat waves, such as the European mega-heat wave in 2003 (Ciais et al., 2005).

These unprecedented climate extremes will impact plant growth, community structure, and ecosystem functions and services in fundamentally different ways from that the normal climatic variability does. Several recent reviews synthesized plant phenological and physiological processes (Reyer et al., 2013) and ecosystem carbon cycle (Reichstein et al., 2013; van der Molen et al., 2011) in response to extreme climate, which greatly advance our understanding on those subjects. Being distinguished from those efforts, this review comprehensively summarizes our current understanding on plant responses, particularly productivity and mortality, to extreme climatic events. Specifically, we will (1) introduce different definitions of extreme climatic events, (2) present evidences regarding impacts of climate extremes on plant production and mortality, (3) synthesize physiological, molecular and ecological mechanisms that regulate plant responses to climate extremes, and (4) propose future research effort in

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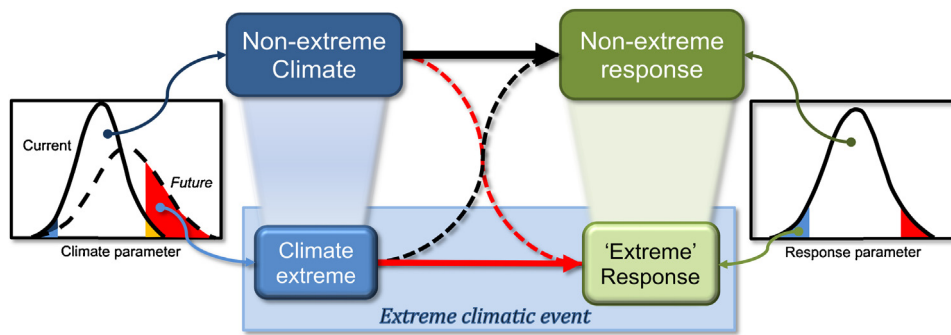


Fig. 1. Conceptual representation of an extreme climatic event. Climate variability can evoke a range of ecological responses (small to extreme, distribution on the right). Changes in climate means or variability may result in a response that is well within the range of variability for a system (solid black arrow) or one that is extreme (i.e., exceeds this range, dashed red arrow). Similarly, climate extremes (represented by tails of the distribution on the left) may (solid red arrow) or may not (dashed black arrow) result in an ecological response that is outside the typical or normal range of variability for a system. Here, an 'extreme climatic event' is defined synthetically as involving extremeness in both the climate driver and the ecological response (modified from Smith, 2011). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

studying plant and ecosystem responses to extreme climatic events.

2. Extreme climatic events: definitions

An extreme climatic event has been defined in different ways. One common way is based on statistical quantification of climatic variables. For example, the Intergovernmental Panel on Climate Change (IPCC) defines an extreme climatic event as one event being rarer than the 10th or 90th percentile of climate events within its statistical frequency distribution at a particular place over a certain period of time (IPCC, 2001). The climatological definition, however, has inherent limitations since a statistical climate extreme may not necessarily incur plant responses (Smith, 2011). Gutschick and BassiriRad (2003) offered an organism-based definition of extremity to evaluate the role of extreme events in the physiology, ecology and evolution of organisms. According to their definition, an extreme climatic event is considered extreme only if it substantially exceeds normal acclimation capacities of organisms.

Recently, a synthetic definition is proposed to represent 'extremeness' in both driving and response variables. Smith (2011) defined an extreme climatic event is an episode or occurrence in which a statistically rare or unusual climatic condition alters ecosystem structure and/or function well outside the bounds of typical or normal responses. Reichstein et al. emphasized the impact perspective further and defined climatic extremes as "conditions where an ecosystem function is higher or lower than a defined extreme percentile and traceable to anomalous meteorological variables (Reichstein et al., 2013). These extreme ecological responses are expected to result from widespread mortality or reduced growth leading to alterations in species composition and consequently large changes in ecosystem structure and function. These definitions emphasize the context-dependency that an extreme climatic event depends on both the historical climate record and the type of impacts, effects or outcomes with respect to natural variability in the system. Thus, the synthetic definition considers both the driver (occurrence) and response (effect) perspectives (Fig. 1).

Climatologically, an extreme event can be defined by the tails of a distribution for a climate parameter (e.g. mean, maximum, minimum temperature or precipitation) (Fig. 1). As a consequence, identification of an extreme climatic event depends on the available climate record. A climate extreme in a 50-year record may not be one in a 100-year record due to changes in statistical distribution of the climate variable. In contrast, organism-based definition of

extremity has to consider the type of climate extreme, the system in question, and the time frame of examination. A 100-year drought causes mortality of individuals or entire populations, which is considered to be an extreme event. However, the mortality of individuals or populations may not necessarily lead to an ecological response beyond the typical range of variability for an ecosystem (Smith, 2011). Such responses may not be distinguishable from background variability (Fig. 1).

The above definitions of extreme events are useful to guide research on plant responses. However, most publications on this topic might not clearly explain which definition they used (Smith, 2011). Thus, although this paper may not represent an exhaustive review on every type of extreme event, it seeks to highlight current understanding of plant responses, especially the responses of plant production and mortality, to climate extremes.

3. Plant production in response to extreme climate

Numerous manipulative experiments have been conducted to study warming impacts on plant growth and ecosystem production but only rarely do experiments to simulate heat waves. In general, experimental warming stimulates plant growth and net ecosystem production in experimental studies (Luo, 2007; Rustad et al., 2001). Model studies indicate that future climate warming is expected to enhance plant growth in temperate ecosystems and to increase carbon sequestration (Bonan, 2008; Piao et al., 2009). However, when climate or weather extremes such as heat waves occur, plant growth and ecosystem primary production usually decrease (Reichstein et al., 2013). For example, a European mega heat-wave in 2003 resulted in a 30% reduction in gross primary productivity (Ciais et al., 2005). The radial tree growth was greatly reduced by 10–43% by heat-wave in coniferous forest in summer 2003 (Pichler and Oberhuber, 2007). With the extreme high temperature becoming more frequent, it is predicted that the forest production reduction will continue to intensify in coming decades (Williams et al., 2012).

Under climate warming scenarios, the earlier onset of growing season may cause de-hardening, leading to an increased risk of frost damage (Kreyling et al., 2012; Taulavuori et al., 1997, 2004). Frost hardiness can protect plants over winter, but de-hardening usually occurs within a few hours, leaving the plants vulnerable to short-term frost events during the growing season. The more frequent freeze–thaw cycles, caused by climate warming during winter and associate with de-hardening during warm days, may also lead to frost damage at further sub-zero temperatures (Bokhorst et al., 2010; Walter et al., 2013). A snowless winter in

northern ecosystems may lead to frost damage, desiccation and photo-oxidation (Taulavuori et al., 2011). Widely observed reductions of plant production over large areas due to spring freeze were well documented in the eastern US (Gu et al., 2008). But manipulative experiments or modeling studies on frost impacts on ecosystem production are rare so far.

The wide spread of drought can induce large-scale tree decline episodes in the temperate regions (Breda et al., 2006) and turn temperate ecosystems into carbon sources, contributing to positive carbon-climate feedback (Schwalm et al., 2012). In Amazonian rainforests, the 2005 drought decreased plant production in association of increased mortality and reduced growth (Phillips et al., 2009). However, a field experiment showed that a severe drought treatment did not appreciably change above- and below-ground primary production across five years of the study in a grassland in central Europe (Jentsch et al., 2011). In this study, drought was defined as the number of consecutive days with <1 mm daily precipitation in the experiment. Apparently, the drought experiment satisfied the climatological definition of the extreme event and changed plant physiological processes but did not significantly change plant production, and thus would not be considered as an extreme climatic event (Smith, 2011).

Flooding events or heavy rainfall are expected to occur more frequently with large influences on plant growth (Vervuren et al., 2003). In fully or partially submerged plants, impeded gas exchange and reduction of available photosynthetic light are primary constrained to limit oxygen availability and thus restrict plant photosynthesis and production (Voeselek et al., 2006). For most flood-intolerant species, concentrations of macronutrients (N, P, K) and total amounts absorbed are generally lowered under flooding due to inhibition of root growth or suppression of root metabolism, which also contribute to the decreased plant production (Kozłowski, 1984). However, experimental evidence and mechanistic understanding are still limited on plants and ecosystem functions in response to heavy rainfall.

4. Plant mortality and population dynamics in response to extreme climate

Plant mortality has become widely spread across all biomes and plant functional types as a result of frequent extreme climatic events. Increased tree mortality and die-offs triggered by drought and/or high temperatures has been well documented on all continents (McDowell et al., 2008), such as in the tropical moist forests of Borneo (Van Nieuwstadt and Sheil, 2005), Canada's boreal forest (Peng et al., 2011), and Western United States (van Mantgem et al., 2009). However, it is often difficult to separate these mortality and die-off events from other factors, such as pest outbreaks which often co-occur with drought. Besides drought and high temperature, frost and flooding also cause large area plant mortality. The 2007 eastern US spring freeze caused widespread devastation of crops and natural vegetation (Gu et al., 2008), and the extensive flooding of the river Rhine in 1999 cause large damage and mortality of adult trees (Kramer et al., 2008).

Climate extremes can cause differential survivorship among species due to their different sensitivity, leading to changes in community structure and plant distributions (Engelbrecht et al., 2007; Miriti et al., 2007). Manipulative experiments showed great changes in population dynamics and community structure in response to climatic warming in grasslands (Sherry et al., 2012) and tundra ecosystems (Chapin et al., 1996), with a consequent woody invasion in herb-dominated ecosystems (Chapin et al., 1996; Harte and Shaw, 1995). The increase in shrubs and graminoids could reduce the competitive performance of other members of the

community and therefore change the competitive hierarchy within a community (Niu and Wan, 2008).

Climate extremes may not always induce vegetation shifts and community structure changes (Lloret et al., 2012). For instance, the Spanish Forest Inventory data showed relatively small effects of drought on mortality rate in Scots pine (*Pinus sylvestris*) (Vila-Cabrera et al., 2011). The simulated extreme drought in an experiment study did not cause any shift in the absolute abundance of species, or any compositional change in Northern Europe grassland within five years of the study (Jentsch et al., 2011), which were primarily due to the drought-induced complementary plant-plant interactions, shifts in flower phenology, and decreased invasibility. The minor changes in community structure in the experimental studies may be partly due to the short-term duration while the vegetation dynamics are determined by long-term processes. Particularly, the plant communities dominated by long-lived species often experience a pervasive inertia to species replacement and they recover relatively easily after climate extremes or disturbances (Clark, 2010). Thus, it is essential to carry out long-term experiments and spatially representative monitoring of vegetation to study responses of community structure to climate extremes (Luo et al., 2011).

The above mentioned diverse responses of plant growth and mortality to climate extremes likely result from different severities of the extremes, background conditions of ecosystems, species or vegetation types or management, biodiversity and other ecosystem regulatory mechanisms (Jentsch et al., 2011; Kreyling et al., 2008; Taulavuori et al., 2010). The various responses indicate different thresholds or tipping points (beyond which disasters may occur) for different variables and ecosystems. But so far, it is very rare that multiple plant growth and ecosystem functions are measured in a single study or compared among vegetation types to examine the differential threshold for climate extreme impacts. Moreover, different methodological approaches may also cause various conclusions, which are exemplified by the different phenology responses to climate change in experiment vs. observation approaches (Wolkovich et al., 2012). The combination of experimental, observational, and/or modeling approaches will be more powerful to capture plant responses to climatic extremes than any individual approaches (Reyer et al., 2013).

5. Physiological and molecular mechanisms underlying plant response to climate extremes

Plants trigger a variety of physiological and molecular mechanisms to regulate responses to extreme climate (Fig. 2). Photosystem II (PSII), for example, is often considered the most heat-sensitive component of the photosynthetic apparatus (Allakhverdiev et al., 2008). Pre-treatment with short-time heating can increase tolerance of PSII to elevated temperatures and short-time exposure to strong light can increase the thermostability of PSII in plant leaves (Allakhverdiev et al., 2008). This kind of heat tolerance will protect photosynthetic machinery from heat stress by accumulating heat-shock proteins.

The magnitude of plant responses to extreme temperature may be also related to acclimation or adaptation capability, which varies with plant species (Fig. 2). One primary type of thermal acclimation is an upward shift of the optimal temperature of photosynthesis, which likely results from the photosynthetic apparatus becoming more tolerant to heat stress (Niu et al., 2008). Plants also have photoprotection mechanisms that are critical for acclimation and survivorship during heat waves. Some species resist heat waves by accumulating tocopherols and some specific carotenoids together with the down-regulation of photochemical efficiency (García-Plazaola et al., 2008). The ability to overcome the reactive oxygen

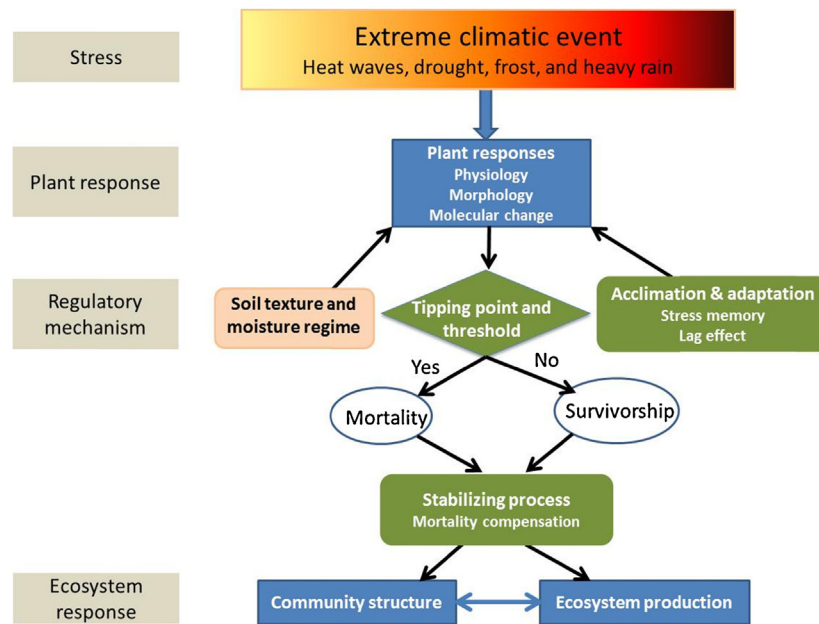


Fig. 2. Conceptual figure of plant responses to extreme climatic events at individual plant level, community and ecosystem levels and the corresponding regulatory mechanisms.

production that generates during heat stress is one of the mechanisms involved in heat tolerance (García-Plazaola et al., 2008). However, it is not well quantified when and at what levels of heat stress plants may pass their thresholds of acclimation and adaptation that may result in mortality.

Extreme droughts increase plant mortality likely by hydraulic failure and carbon starvation, with their relative importance depending on the intensity and duration of stress (McDowell et al., 2008). The hydraulic-failure hypothesis predicts that reduced soil water supply, coupled with high evaporative demand, causes xylem cavitation and desiccation of plant tissues (Davis et al., 2002). The carbon-starvation hypothesis predicts that stomatal closure to prevent water loss diminishes photosynthetic carbon uptake, which, together with continued metabolic demand for carbohydrates, causes plant starvation (McDowell, 2011). These two hypotheses have stimulated much discussion (McDowell and Sevanto, 2010; Sala et al., 2010). An integrated mechanism was recently proposed that avoidance of drought-induced hydraulic failure via stomatal closure results in carbon starvation and a cascade of downstream effects, leading to plant mortality under drought condition (McDowell and Sevanto, 2010).

Some plants may survive the drought without dying, probably due to high drought resistance of plants. Resistance mechanisms for drought may involve various morphological, physiological, biochemical, and molecular acclimations and adaptations (Fig. 2) (Ciordia et al., 2012). Morphological changes include shrinkage in the size of leaves, decrease in the number of stomata, thickening of leaf cell walls, increase in the number of large vessels, submergence of stomata in succulent plants and in xerophytes, induction of early senescence and increases in root-to-shoot ratio (Jaleel et al., 2009). Physiological acclimation and adaptation include low stomatal conductance and density, slow rates of transpiration or high transpiration efficiency, rapid establishment, early and reduced asynchrony between male and female flowering and maturation, and better accumulation and partitioning of biomass and seed yield (Galmes et al., 2011). While cellular adjustments entail high chlorophyll content, heat shock proteins and dehydrins low osmotic potential by producing compatible compounds, and mechanisms of desiccation-tolerance (Hasanuzzaman et al., 2013).

Various climate extremes, such as drought, frost, heatwave and heavy rainfall, commonly cause cellular damage and secondary stresses, such as osmotic and oxidative stress (Vinocur and Altman, 2005). These initial stress signals may trigger the downstream signaling process and transcription controls (Fig. 3). The latter will activate stress-responsive mechanisms to re-establish homeostasis and to protect and repair damaged proteins and membranes. Inadequate responses at one or more steps in the signaling and gene activation processes might ultimately result in cell death, being primarily due to the irreversible changes in cellular homeostasis and the destruction of functional and structural proteins and membranes (Vinocur and Altman, 2005). The stress tolerance may occur when plants re-establish cellular homeostasis, functional and structural protection of proteins and membranes (Fig. 3).

6. Ecological mechanisms underlying plant responses to extreme climate

Climate extremes can trigger a suite of ecological processes to regulate plant and ecosystem responses (Fig. 2). At the individual level, a plant has the capability of so-called stress memory by which it can remember the past stress experienced to influence the present or future responses to environmental stress (Tahkokorpi et al., 2007; Walter et al., 2013). Plant stress memory emerges as a plant modifies its performance upon stress exposure and persists after the stress ceased. When climate extremes repeatedly occur, a plant may not return to its previous state during the period between two extreme events, thus affecting plant responses to the future stress (Walter et al., 2013). The stress memory may lead to a faster response and increase plant tolerance to a next extreme event.

Similar to a stress memory in plant ecophysiology, plants and ecosystems also have lag or carry-over effects. For example, a severe frost often had little apparent effects in the first year and increased mortality of dwarf-shrubs in subsequent years (Jentsch et al., 2009). The response of trees to drought may become progressively more apparent for several years after the drought event as mortality often increased over time (Bigler et al., 2007). Such lagged responses are not easily detectable right after the event and may explain the

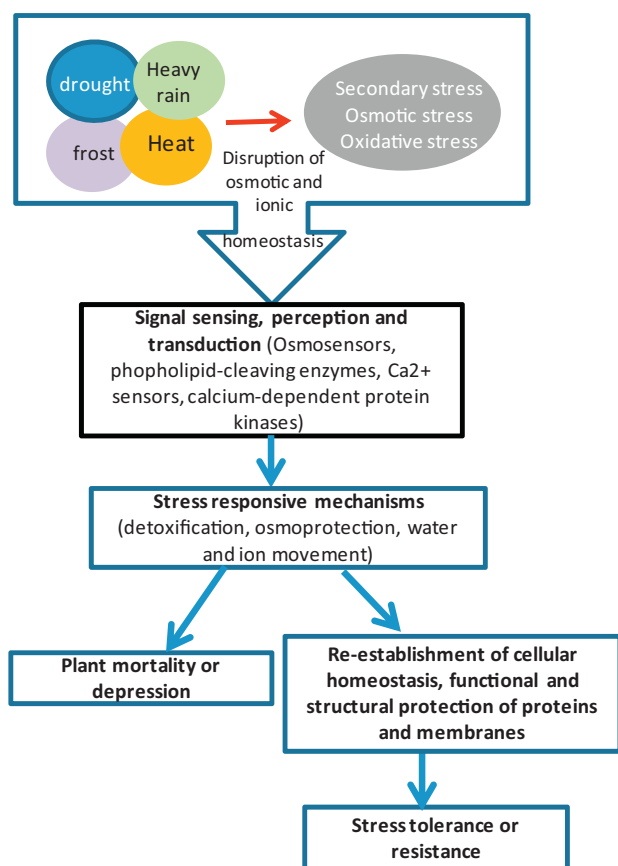


Fig. 3. The complexity of the plant in responses to extreme climatic event (modified from Vinocur and Altman, 2005).

findings of reduced resilience upon repeated stress events. The lag effects of extreme events can carry over for up to years on plant biomass production (Arnore et al., 2008; Sherry et al., 2008), autotrophic and heterotrophic respiration (Zhou et al., 2010), and plant phenology (Sherry et al., 2011). So, the temporal scale of climate extremes and their impacts are also important issues for further study.

At the community level, stabilizing processes can minimize and counteract the effects of extreme events to reinforce community resilience (Fig. 2). Lloret et al. (2012) proposed a demographic framework based on the balance between the event-induced plant mortality and the enhanced recruitment after the event. Mortality compensation may occur by increasing future survivorship due to lowered competition resulting from reduced density in affected stands or to released antagonism when pathogens or predators are vulnerable to the event. For example, decreased plant density under climate extremes can reduce competition, at least at the intra-specific level, to lower the vulnerability of the population to future climate extremes (Vila-Cabrera et al., 2011). Recruitment is usually enhanced due to gap openings after extreme-caused mortality, or due to the new conditions that may be more favorable for seedling establishment, or the enhanced mutualistic interactions (pollination, dispersal) (Hiernaux et al., 2009).

At the ecosystem level, responses of plant production to an extreme precipitation are also strongly regulated by soil moisture (Knapp et al., 2008) and soil texture (Weng and Luo, 2008). Soil acts as a buffer to store water in a quantity that varies with soil textures, such as sand, sandy loam, loam, silt loam, and clay loam. For each soil texture, there is one set of upper and lower water stress thresholds (i.e., field holding capacity and permanent wilting point, respectively) for ecological processes (Porporato et al., 2004).

When the soil water content is above the upper threshold, waterlog stress occurs. When the soil water content is below the lower threshold, severe drought stress happens. In either case, photosynthesis and growth are reduced. When the soil water level is between the lower and upper thresholds, there usually is a strong relationship between soil water content and rates of plant or ecosystem processes (Knapp et al., 2008).

In summary, climate extremes directly influence plant physiology, triggering a suite of acclimation and adaptation processes to eventually determine different response magnitudes. Heat stresses initially elevate metabolic rates and then induce various acclimatory and adaptive processes. Eventual responses of plants to heat stress depend on the magnitude of the heat stress and the capacity of plants to acclimate and adapt. Severe droughts initially cause stomata closure, depressed photosynthesis, and increased water tension within xylem. In response, plants may adjust root growth, decrease stomatal conductance and density, increase heat shock protein and dehydrins. If severe drought induces hydraulic failure and starvation, mortality increases. Some ecological mechanisms, such as the lagged responses, stress memory, and soil water storage could also regulate plant responses to climate extremes (Fig. 2). At community and ecosystem level, plant communities also have stabilizing mechanisms, which counteracts the effects of the climate extremes, reinforcing community resilience and cause little changes in ecosystem production (Fig. 2).

7. Future research on plant responses to extreme events

Responses of plant growth and mortality to climate extremes are exceedingly variable. To identify causes of such variable responses, we need to define extreme climatic events under plant perspectives and evaluate different response patterns of various processes to climate extremes. Future research can effectively reveal fundamental mechanisms if we conduct more manipulative experiments in network of studies at multiple sites over different regions.

1. *Defining climatic extreme events:* To better understand impacts of climate extremes on plants and ecosystems, we first need to clearly define and identify climatic extreme events. There are many ways to identify climate extremes. Climatic drought, for example, can be defined as extreme years of annual precipitation amounts beyond either upper or lower five percentiles over a long-term record, extreme seasonal or monthly precipitation amounts, durations of rainless drought spreads, or extreme rainfall sizes. Besides those climatic statistics, we also need to evaluate those extreme events under the perspective of relevance to plant or ecosystem structure and functions (Smith, 2011). As a consequence, the definition of a drought extreme event, for example, will differ widely in different environments. A 20-day drought spread may be an extreme event for tropical rainy forest but is normal in a deserts area. So, it is essential to develop some statistical and probabilistic techniques to define extreme climatic events under plant and ecosystem perspectives.

2. *Evaluation of relative impacts of various extreme events on ecosystems.* Not all rare climatological events could cause severe impacts on plants and ecosystems. For example, major rainfall events in extreme wet years (or the lack of them in extreme drought years) may have major impacts on runoff and lake water recharge but less on carbon cycle. It is a challenge to evaluate how severely and at which time scales individual extreme events influence different ecosystem response variables (Smith, 2011). Processes at different hierarchical levels of biology likely respond to the same extreme events differently. Thus, we have to clearly define response

variables in question and then evaluate how they may respond to various extreme events before we conduct experiments.

3. Manipulative experiments to uncover underlying mechanisms. Manipulative experiments may be designed according to extreme events that happen in the real world of a region or to create artificial events that are extreme enough to push ecosystems over tipping points. In the latter design, we may discover thresholds of ecosystem state changes. Moreover, we may conduct laboratory experiments to evaluate plant responses and their underlying mechanisms in accompany with field manipulative experiments. Laboratory experiments alone are useful to examine plant response to environmental stress, but responses of individual plants in isolation usually could not reflect ecosystem responses. So, any long-term field experiments in natural plant communities will be very valuable to reveal plant and ecosystem responses to climatic extremes. There are very limited ecosystem level experiments on climate extremes (Beier et al., 2012; Jentsch and Beierkuhnlein, 2008; Jentsch et al., 2011). The interactions between ecosystem ecology and plant biology will help gain insights into real-world responses of vegetation and ecosystems to climate extremes and improve understanding the underlying mechanisms.

4. Networks of study sites to identifying spatial distributions of impacts of extreme events. Climatic extreme events happen in different forms in different regions. The heterogeneity in extreme events likely generates different impacts in different ecosystems. Thus, we need to estimate spatial distributions and temporal frequency of ecosystem responses to extreme events and the subsequent recovery processes after the events. It can be achieved by networks of experiments at different sites over a region or the globe. These networks will improve our ability to integrate local-scale data to the regional and continental scales and to reveal general mechanisms under diverse ecosystem responses to heterogeneous extreme events. To maximize the value of networks of studies, it is necessary to standardize experimental designs and methods for measuring ecological responses. Moreover, these networks will be greatly enhanced if they can be coordinated with modeling studies (Luo et al., 2011). Conditioned models can be used to predict ecosystem responses to future climatic extreme events in particular and climate change in general.

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