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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.

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; Orlowsky 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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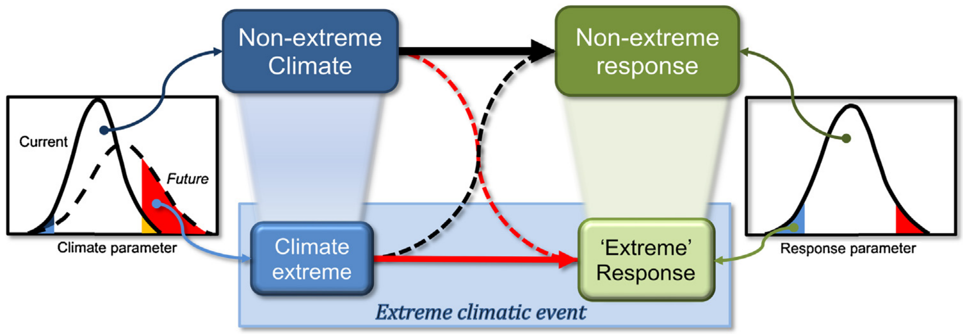

Fig. 1. Conceptual representation of an extreme climatic event. Climate variability can evoke a range of ecological responses (small to extreme, distribution on the right). Changes in climate means or variability may result in a response that is well within the range of variability for a system (solid 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