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Heat stress in cereals: Mechanisms and modelling

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ABSTRACT

Increased climate variability and higher mean temperatures are expected across many world regions, both of which will contribute to more frequent extreme high temperatures events. Empirical evidence increasingly shows that short episodes of high temperature experienced around flowering can have large negative impacts on cereal grain yields, a phenomenon increasingly referred to as heat stress. Crop models are currently the best tools available to investigate how crops will grow under future climatic conditions, though the need to include heat stress effects has been recognized only relatively recently. We reviewed literature on both how key crop physiological processes and the observed yields under production conditions are impacted by high temperatures occurring particularly in the flowering and grain filling phases for wheat, maize and rice. This state of the art in crop response to heat stress was then contrasted with generic approaches to simulate the impacts of high temperatures in crop growth models. We found that the observed impacts of heat stress on crop yield are the end result of the integration of many processes, not all of which will be affected by a "high temperature" regime. This complexity confirms an important role for crop models in systematizing the effects of high temperatures on many processes under a range of environments and realizations of crop phenology. Four generic approaches to simulate high temperature impacts on yield were identified: (1) empirical reduction of final yield, (2) empirical reduction in daily increment in harvest index, (3) empirical reduction in grain number, and (4) semi-deterministic models of sink and source limitation. Consideration of canopy temperature is suggested as a promising approach to concurrently account for heat and drought stress, which are likely to occur simultaneously. Improving crop models' response to high temperature impacts on cereal yields will require experimental data representative of field production and should be designed to connect what is already known about physiological responses and observed yield impacts.

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1. Introduction

Increased climate variability and higher mean temperatures are expected across many world regions (Weisheimer and Palmer, 2005; Tebaldi et al., 2006; Battisti and Naylor, 2009; Field et al., 2012) and are likely to cause large negative impacts on crop productivity (Porter and Semenov, 2005). Empirical evidence increasingly shows that short episodes of high temperature can have large negative impacts on crop yields (Reidsma et al., 2009; Schlenker and Roberts, 2009; Lobell et al., 2013). At a global scale, wheat yields have been negatively impacted by rising temperatures, as detected by Lobell and Field (2007) between 1961 and 2002. The negative trend of decreasing wheat yields with more frequent high temperature extremes during sensitive reproductive stages is apparent across many regions, as found by Gourdji et al. (2013) for recent decades (1980–2011) across Central and South Asia and South America. Wheat yields in Mexico show a significant negative response to higher night-time temperatures (Lobell et al., 2005). Likewise for maize, an analysis of the past 50-years of historical yields in France revealed that since approximately 2000, daily maximum temperatures explain as much yield variability as precipitation (Hawkins et al., 2013), with the cumulative number of days with a maximum temperature over 32 °C associated with yield reductions. Lobell et al. (2011) determined maize kernel set was reduced by 1% per degree day (and 1.7% per degree day under drought stressed conditions) when daily temperatures were above a threshold 30 °C in Sub-Saharan Africa. A national panel analysis of county level maize yields in the United States detected negative impacts on maize yields when daily temperatures were above 29 °C (Schlenker and Roberts, 2009). Evidence in rice suggests that this crop is also sensitive to increasing nighttime temperatures, expected to increase with climate change (Tebaldi et al., 2006). In an analysis of historical station data across China for the period 1981–2000, rice yields declined with higher nighttime temperatures, decreasing at a rate of 4.6% per 1 °C increase in minimum temperature (Tao et al., 2006). The decline in an indica rice varietals' yield over a 25-year period in the Philippines was associated with an increase in minimum nighttime temperature but not correlated with the concurrent but smaller increase in daily maximum temperature (Peng et al., 2004). As the majority of cereal production, particularly rice and maize, now occurs at mean temperatures above the optimal (Hatfield et al., 2011) increases in global mean temperature would augment yield reductions (Lobell and Gourdji, 2012).

The term heat stress is increasingly used to describe these negative impacts of high temperature on plant growth, though a definitive definition has yet to emerge in the literature and remains elusive. Heat stress has been used to refer to brief episodes of high temperature lying outside of the range typically experienced (Porter and Gawith, 1999; Luo, 2011; Moriondo et al., 2011). Porter and Semenov (2005) and Wheeler et al. (2000) emphasize that negative yield impacts are greatest when high temperatures are experienced during the reproductive phases centered on flowering. Some authors define a high temperature event as heat stress if it results in large, irreversible yield reductions (Wahid et al., 2007). Attribution of yield losses is frequently explained by a reduction in the number of viable seeds produced (Wheeler et al., 2000; Moriondo et al., 2011) or accelerated leaf senescence that reduces yields by shortening the duration of grain filling (Al-Khatib and Paulsen, 1984; Asseng et al., 2011; Lobell et al., 2012). Finally, other authors have defined heat stress as the departure from the regular linear yield response to rising temperatures that occurs when a threshold is surpassed, apparent in the analysis of large panel datasets (Schlenker and Roberts, 2009; Lobell et al., 2011).

The lack of convergence in definitions may simply reflect the need to illustrate specific aspects or levels of detail in different cases. However, it likely also reflects the limitations of our understanding of the mechanisms of high temperature impacts on yield in field crops. Such impacts are the end result of the integration of many processes that operate at the organelle and lower levels all with differing sensitivities to temperature (Sage and Kubien, 2007) and their interactions with other temperature sensitive processes such as transpiration, assimilation and partitioning (Ferrise et al., 2011). These processes are generally studied in isolation (Wahid et al., 2007; Barnabás et al., 2008) and are difficult to abstract to conditions typical in the field. Secondly, the relatively few field scale experimental trials on heat stress have imposed high temperature at different periods, for differing durations and levels, under varying environmental conditions and using different varieties (Lobell et al., 2012), sometimes leading to what seem to be conflicting conclusions. Further, while at the field and larger scales, heat stress is frequently understood to represent a non-linear temperature response, many of the underlying individual mechanisms may not be deviating from their linear response (e.g. the acceleration of crop development with elevated temperatures that results in shorter duration of grain filling). For the remainder of this paper, we use the term very broadly to mean yield reductions resulting from high temperature whose mechanism and impacts are hypothesized to vary with crop, region and the scale considered.

This complexity suggests an important role for crop models to systematize the effects of many processes under a range of environments. However, despite the evidence of the role of high temperatures in reducing grain number (Porter and Gawith, 1999; Wheeler et al., 2000), a key determinant of final yield in cereals (Cirilo and Andrade, 1994; Otegui, 1995; Ferris et al., 1998; Fischer et al., 1998; Hayashi et al., 2012), crop model simulation efforts to date have focused largely on how high temperature accelerates leaf senescence in wheat (Asseng et al., 2011; Lobell et al., 2012) or