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Temperature extremes: Effect on plant growth and development

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ABSTRACT

Temperature is a primary factor affecting the rate of plant development. Warmer temperatures expected with climate change and the potential for more extreme temperature events will impact plant productivity. Pollination is one of the most sensitive phenological stages to temperature extremes across all species and during this developmental stage temperature extremes would greatly affect production. Few adaptation strategies are available to cope with temperature extremes at this developmental stage other than to select for plants which shed pollen during the cooler periods of the day or are indeterminate so flowering occurs over a longer period of the growing season. In controlled environment studies, warm temperatures increased the rate of phenological development; however, there was no effect on leaf area or vegetative biomass compared to normal temperatures. The major impact of warmer temperatures was during the reproductive stage of development and in all cases grain yield in maize was significantly reduced by as much as 80–90% from a normal temperature regime. Temperature effects are increased by water deficits and excess soil water demonstrating that understanding the interaction of temperature and water will be needed to develop more effective adaptation strategies to offset the impacts of greater temperature extreme events associated with a changing climate.

1. Introduction

Rate of plant growth and development is dependent upon the temperature surrounding the plant and each species has a specific temperature range represented by a minimum, maximum, and optimum. These values were summarized by Hatfield et al. (2008, 2011) for a number of different species typical of grain and fruit production. The expected changes in temperature over the next 30–50 years are predicted to be in the range of 2–3 °C Intergovernmental Panel Climate Change (IPCC) (2007). Heat waves or extreme temperature events are projected to become more intense, more frequent, and last longer than what is being currently been observed in recent years (Meehl et al., 2007). Extreme temperature events may have short-term durations of a few days with temperature increases of over 5 °C above the normal temperatures. Extreme events occurring during the summer period would have the most dramatic impact on plant productivity; however, there has been little research conducted to document these effects as found by Kumudini et al. (2014). A recent review by Barlow et al. (2015) on the effect of temperature extremes, frost and heat, in wheat (*Triticum aestivum* L.) revealed that frost caused sterility and abortion of formed grains while excessive heat caused reduction in grain number and reduced duration of the grain-filling period. Analysis by Meehl et al. (2007) revealed that daily minimum temperatures will increase more rapidly than daily maximum temperatures leading to the increase in the daily mean temperatures and a greater likelihood of extreme events and these changes could have detrimental effects on grain yield. If these changes in temperature are expected to occur over the next 30 years then understanding the potential impacts on plant growth and development will help develop adaptation strategies to offset these impacts.

1.1. *Temperature responses*

Responses to temperature differ among crop species throughout their life cycle and are primarily the phenological responses, i.e., stages of plant development. For each species, a defined range of maximum and minimum temperatures form the boundaries of observable growth. Vegetative development (node and leaf appearance rate) increases as temperatures rise to the species optimum level. For most plant species, vegetative development usually has a higher optimum temperature than for reproductive development. Cardinal temperature values for selected annual (non-perennial) crops are given in Hatfield et al. (2008, 2011) for different species. If we depict the range of temperatures in the following diagram (Fig. 1) then the definition of extreme temperatures affecting plant response will be species dependent. For

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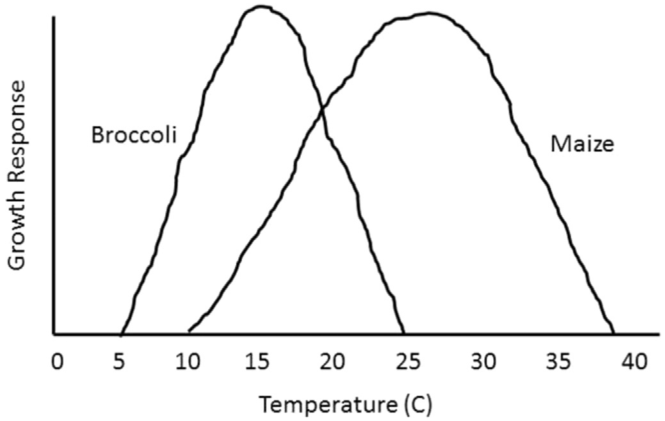

Fig. 1. Temperature response for maize and broccoli plants showing the lower, upper and optimum temperature limits for the vegetative growth phase.

example, an extreme event for maize (*Zea mays* L.) will be warmer than for a cool season vegetable (broccoli, *Brassica oleracea* L.) where the maximum temperature for growth is 25 °C compared to 38 °C. In understanding extreme events and their impact on plants we will have to consider the plant temperature response relative to the meteorological temperature.

Faster development of non-perennial crops results in a shorter life cycle resulting in smaller plants, shorter reproductive duration, and lower yield potential. Temperatures which would be considered extreme and fall below or above specific thresholds at critical times during development can significantly impact productivity. Photoperiod sensitive crops, e.g., soybean, would also interact with temperature causing a disruption in phenological development. In general, extreme high temperatures during the reproductive stage will affect pollen viability, fertilization, and grain or fruit formation (Hatfield et al., 2008, 2011). Chronic exposures to extreme temperatures during the pollination stage of initial grain or fruit set will reduce yield potential. However, acute exposure to extreme events may be most detrimental during the reproductive stages of development.

The impacts of climate change are most evident in crop productivity because this parameter represents the component of greatest concern to producers, as well as consumers. Changes in the length of the growth cycle are of little consequence as long as the crop yield remains relatively consistent. Yield responses to temperature vary among species based on the crop's cardinal temperature requirements. Warming temperatures associated with climate change will affect plant growth and development along with crop yield.

1.2. *Temperature extremes in climate*

One of the more susceptible phenological stages to high temperatures is the pollination stage. Maize pollen viability decreases with exposure to temperatures above 35 °C (Herrero and Johnson, 1980; Schoper et al., 1987; Dupuis and Dumas, 1990). The effect of temperature is enhanced under high vapor pressure deficits because pollen viability (prior to silk reception) is a function of pollen moisture content which is strongly dependent on vapor pressure deficit (Fonseca and Westgate, 2005). During the endosperm division phase, as temperatures increased to 35 °C from 30 °C the potential kernel growth rate was reduced along with final kernel size, even after the plants were returned to 30 °C (Jones et al., 1984). Exposure to temperatures above 30 °C damaged cell division and amyloplast replication in maize kernels which reduced the size of the grain sink and ultimately yield (Commuri and Jones, 2001). Rice (*Orzya sativa* L.) shows a similar temperature response to maize because pollen viability and production declines as daytime maximum temperature ($T_{\max}$) exceeds 33 °C and ceases when $T_{\max}$ exceeds 40 °C (Kim et al., 1996). Current cultivars of rice flower near mid-day which makes Tmax a good indicator of heat-stress on spikelet sterility. These exposure times occur quickly after anthesis and exposure to temperatures above 33 °C within 1 − 3 h after anthesis (dehiscence of the anther, shedding of pollen, germination of pollen grains on stigma, and elongation of pollen tubes) cause negative impacts on reproduction (Satake and Yoshida, 1978). Current observations in rice reveal that anthesis occurs between about 9 to 11 am in rice (Prasad et al., 2006b) and exposure to high temperatures may already be occurring and will increase in the future. There is emerging evidence that differences exist among rice cultivars for flowering times during the day (Sheehy et al., 2005). Given the negative impacts of high temperatures on pollen viability, recent observations from Shah et al. (2011) suggest flowering at cooler times of the day would be beneficial to rice grown in warm environments. They proposed that variation in flowering times during the day would be a valuable phenotypic marker for high-temperature tolerance. As daytime temperatures increased from 30 to 35 °C, seed set on male-sterile, female fertile soybean (*Glycine max* (L.) Merr.) plants decreased (Wiebbecke et al., 2012). This confirms earlier observations on partially male-sterile soybean in which complete sterility was observed when the daytime temperatures exceeded 35 °C regardless of the night temperatures and concluded that daytime temperatures were the primary factor affecting pod set Caviness and Fagala (1973). Crop sensitivity to temperature extremes depends upon the length of anthesis. Maize, for example, has a highly compressed phase of anthesis for 3 − 5 days, while rice, sorghum (*Sorghum bicolor* L. Moench.*)* and other small grains may extend anthesis over a period of a week or more. Inn soybean, peanut (*Arachis hypogaea* L.), and cotton (*Gossypium hirsutum* L.) anthesis occurs over several weeks and avoid a single occurrence of an extreme event affecting all of the pollening flowers. For peanut (and potentially other legumes) the sensitivity to elevated temperature for a given flower, extends from 6 days prior to opening (pollen cell division and formation) up through the day of anthesis (Prasad et al., 2001). Therefore, several days of elevated temperature may affect fertility of flowers in their formative 6-day phase or anthesis. Singh et al. (2015) found differences in the threshold temperature for grain sorghum among genotypes and differences in the percentage of seed set in response to high temperatures. Pollination processes in other cereals, maize and sorghum, may have a similar sensitivity to elevated daytime temperature as rice. Rice and sorghum have exhibited similar sensitivities of grain yield, seed harvest index, pollen viability, and success in grain formation in which pollen viability and percent fertility is first reduced at instantaneous hourly air temperature above 33 °C and reaches zero at 40 °C (Kim et al., 1996; Prasad et al., 2006a, 2006b). Diurnal max/min day/night temperatures of 40/30 °C (35 °C mean) cause zero yield for those two species with the same expected response for maize.

1.3. *Annual crops*

Projected air temperature increases throughout the remainder of the 21st century suggests that grain yields will continue to decrease for the major crops because of the increase temperature stress on all major grain crops (Hatfield et al., 2011). Beyond a certain point, higher air temperatures adversely affect plant growth, pollination, and reproductive processes (Klein et al., 2007; Sacks and Kucharik, 2011). However, as air temperatures rise beyond the optimum, instead of falling at a rate commensurate with the temperature increase, crop yield losses accelerate. For example, an analysis by Schlenker and Roberts (2009) indicated yield