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The effect of high temperature stress on male and female reproduction in plants

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ABSTRACT

Humanity confronts a major transition in the global environment. With the continued rise in atmospheric greenhouse gases, and wide-spread land transformation, the climate of the planet could warm to levels that have not existed for tens of millions of years. Crop yields are particularly vulnerable to high temperatures and plant reproduction is amongst the most sensitive of the physiological components at temperatures above 30 °C. In this review, we examine the effect of high temperatures on plant reproduction in general, and then focus on heat-induced failure of male and female reproduction in crop and model plant species in order to evaluate the patterns and mechanisms controlling heat sterility responses. The main objective is to provide breeders and molecular engineers with an understanding of the bottlenecks for successful reproductive development at high temperatures. Although numerous stages of male and female reproduction are impacted by elevated temperatures, the collective body of research supports the view that the uninucleate stage of male reproductive development is highly sensitive to levels of heat stress currently experienced by many crop species. Thus, high priority should be given to identification of mechanisms leading to high temperature sensitivity of this stage of development.

1. Introduction

Humanity confronts a major transition in the global environment. With the continued rise in atmospheric greenhouse gases, and wide-spread land transformation, the climate of the planet could warm to levels that have not existed for tens of millions of years (Masson-Delmotte et al., 2013). Assuming business-as-usual emissions scenarios for greenhouse gases, atmospheric CO_2 levels will double-to-triple above current values of 400 ppm within two centuries which in turn will warm the global climate by a mean of 2.5 to 8 °C by the year 2200 (Stocker et al., 2013). Such warming is not unprecedented in Earth's history; however, it is occurring more rapidly than exists in the geological record, and in combination with multiple other changes of major global significance (Sala et al., 2000; Masson-Delmotte et al., 2013). Such changes include increases in ground-level (trophospheric) ozone concentrations, deposition of nutrients that alter soil biogeochemistry, invasions by exotic species, widespread land conversion, and the direct effects of atmospheric CO_2 enrichment on plants and insects (Vitousek, 1994; Long et al., 2004; Ashmore, 2005; Foley et al., 2005; Long and Ort, 2010). Together, these global change drivers threaten to overwhelm the resilience of natural systems and human society, with consequences that will challenge human welfare (Parry et al., 2007; Rockström et al., 2009). Agriculture, in particular, is highly vulnerable to global change as the crops we depend upon are negatively impacted by a number of the drivers, most notably climate change (Easterling et al., 2007; Schlenker and Roberts, 2009; Lobell et al., 2014). Unlike natural systems, however, agriculture is under direct human control, and thus each element of a crop production system can be manipulated to offset deleterious impacts of global change, and in some cases, exploit opportunities that may arise in a globally-altered world (for example, higher atmospheric CO_2 can be exploited to boost photosynthesis and productivity) (Ainsworth et al., 2008; Lobell, 2014; Zhu et al., 2010).

The likelihood that agriculture can adapt to global change will depend upon an understanding of how predicted changes will impact agricultural crops and management systems (Deryng et al., 2014; Lobell and Tebaldi, 2014; Siebert and Ewert, 2014). Such understanding will enable people to target the most vulnerable aspects of the cropping system and to focus on developing appropriate solutions (Ainsworth et al., 2008; Lobell, 2014). At the crop level, this will require a detailed understanding of the mechanisms of plant responses to global climate change, including the genetic controls over responses to combinations of heat, drought and

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elevated atmospheric CO_2 (Long and Ort, 2010; Lobell and Gourdji, 2012). Among the global change responses particularly well studied are the effects of climate warming and atmospheric CO_2 enrichment on photosynthesis, respiration, and growth (Long et al., 2004; Ainsworth et al., 2008). While these responses are noteworthy, they are not likely the most critical threat to food security. Instead, plant reproduction, appears to be among the most sensitive of the physiological components contributing to yield (Prasad et al., 2002, 2006a,b; Barnabas et al., 2008; Hedhly et al., 2009; Reguera et al., 2012; Lobell and Gourdji, 2012; Harsant et al., 2013; Sanchez et al., 2014). In both warm and cool season crops, reproductive processes are widely noted to fail completely between 30 and 40 °C; by contrast, photosynthesis and vegetative growth of warm season crops (particularly C_4 crops) exhibit a thermal optimum of 30 to 36 °C, and it is not uncommon to observe crops with good vegetative growth and photosynthesis being completely sterile (Peng et al., 2004, 2002, 2006a,b; Cowling and Sage, 1998; Sage and Kubien, 2007; Sage et al., 2011; Harsant et al., 2013; Oort et al., 2014; Sanchez et al., 2014). Indeed, current models of crop responses to climate warming predict that for every 1 °C rise in mean local temperature during the growing season, average grain yields of our major crops such as maize and rice will decline from 5% to 17%, in part due to heat induced sterility (Peng et al., 2004; Sheehy et al., 2006; Hedhly et al., 2009; Challinor et al., 2014; Lobell and Tebaldi, 2014).

It has been argued that plant reproductive sterility is a major threat to global food security in a warming world (Reguera et al., 2012; Bita and Gerats, 2013). If this is the case, substantial effort would be warranted to identify mechanisms controlling the sterility response and develop ways to overcome the problem, be it through selective breeding or genetic engineering of new, heat tolerant varieties, or via adoption of management techniques that avoid exposure to sterilizing events. Here, we survey the literature on the effect of high temperature (HT) on plant reproduction in general. We then review the response of heat stress on male and female reproductive development in crop and model plant species to highlight our current understanding of cellular and molecular mechanisms controlling the heat sterility response. Our main objective is to provide breeders and molecular engineers with an understanding of the bottlenecks for successful reproductive development at HT.

2. High temperature and plant reproduction

2.1. General patterns

The unfavourable influence of HT on crop yields results from injury during development to reproductive units that contribute to harvest index and the responses vary with the duration and severity of the heat stress (Barnabas et al., 2008; Hedhly et al., 2009; Harsant et al., 2013). High temperatures reduce the number of flowering branches that are initiated, and thus the number of flowers per plant (Dawson and Wardlaw, 1989; Allen et al., 1995; Reddy et al., 1992; Young et al., 2004; Prasad et al., 2001, 2002; Harsant et al., 2013). Day time temperatures as low as 30 °C can induce abortion and subsequently abscission of developing floral buds as well as fruits in numerous legumes, (Konsens et al., 1991; Ahmed et al., 1992; Gross and Kigel, 1994; Guilioni et al., 1997; Djanaguiraman et al., 2013), tomato (Levy et al., 1978; Charles and Harris, 1972; Warner and Erwin, 2001), cotton (Reddy et al., 1992), pepper (Aloni et al., 2001), and canola-related species (Angadi et al., 2000; Young et al., 2004; Faraji et al., 2008). Fruit and seed dry weight are also reduced at temperatures ranging from 30 to 38 °C (Wardlaw, 1994; Prasad et al., 2002, 2008; Harsant et al., 2013; Prasad and Djanaguiraman, 2014).

Within developing flowers, male and female organs are sensitive to temperatures ≥30 °C. The impact of HT on the male reproductive development has been the primary focus of crop research for many years as it has been viewed as the most vulnerable (Sharkey and Schrader, 2006; Dolferus et al., 2011). The enhanced sensitivity of the male reproductive process is observed when reciprocal crosses using pollen from plants treated with HT reduces yields significantly more than when female plants treated with the same temperature are the receptor plants (Dupuis and Dumas, 1990; Peet et al., 1998; Young et al., 2004; Endo et al., 2009; Devasirvatham et al., 2012). Moreover, many studies on warm-season crop plants such as rice, sorghum, and soybean demonstrate temperatures in the mid-to-upper 30s °C result in reduced yields that are highly correlated with declines in pollen production as well as viability as indicated by viability stains and assessment of *in vitro* and *in vivo* pollen tube growth (Matsui et al., 1997; Prasad et al., 1999, 2001, 2002, 2003, 2006b; Djanaguiraman et al., 2013; Maruyama et al., 2013; Prasad and Djanaguiraman, 2014; Singh et al., 2015). This severity of the impact of HT on male reproduction and crop yields is best illustrated in rice where high day (≥32 °C) and night (≥29 °C) temperatures drastically reduce or eliminate yields solely through their negative effect on one or more of the sensitive stages of male reproduction (Satake and Yoshida, 1978; Peng et al., 2004; Shah et al., 2011; Laborte et al., 2012; Teixeira et al., 2012; Bagha, 2014; Nguyen et al., 2014). Notably, the major rice growing regions currently experience both high day and night temperatures during flowering (Fig. 1; Peng et al., 2004; Sheehy et al., 2006; Wassmann et al., 2009; Welch et al., 2010; Shah et al., 2011; Laborte et al., 2012; Teixeira et al., 2012; Bagha, 2014).

Although male reproduction has generally been viewed as more sensitive than female reproduction at HT, data indicates that female tissues as well as processes important for development of the male (pollen tube) within female tissues after pollination are also sensitive to HT (Snider and Oosterhuis, 2011; Gupta et al., 2015). The mechanisms regulating failure of male and female reproductive development and post-pollination processes up to the time of fertilization during exposure to HT are not clearly understood. This observation is alarming given the recognized importance of these processes to both current agriculture and sustainability of future agriculture in a warmed-world (Barnabas et al., 2008; Hedhly et al., 2009; Snider and Oosterhuis, 2011; Giorno et al., 2013; Gourdji et al., 2013).

2.2. Anther and pollen development in elevated temperatures

The anther is the region of the male reproductive structure that functions to produce pollen (reviewed in Ma, 2005; Wilson et al., 2011). It is composed of four fused lobes, each made of five cell layers that develop shortly after stamen initiation. Anther and pollen development from meiosis onward is illustrated in Fig. 2. The innermost layer of the anther is where the microspore mother cells develop and each mother cell will undergo meiosis to form uninucleate microspores that then undergo two successive mitotic divisions to give rise to a mature pollen grain. Two cell layers surrounding the microspore mother cells in anthers are the tapetum and the middle layer. Both of these layers are ephemeral and will undergo a programmed cell death after pollen wall development has ensued. The fourth cell layer of the anther, the endothecium, is positioned between the epidermis and middle layer. Endothecial cells as well as the stomium, which is a region of specialized epidermal cells, play crucial roles in anther dehiscence and thus pollen release. Dehydration of anthers facilitates anther opening, a process that is enabled by separation of stomium cells and retraction of the endothecium cells. Endothecial retraction is