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Review

Sensitivity of flowering plant gametophytes to temperature fluctuations

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ABSTRACT

Research on plant responses to temperature stress is receiving increased interest due to the growing awareness about global warming. High and low temperature stresses help establish the narrow geographic distribution of some cultivated plants, the limited geographic extension of some other economically nutritionally important species, and also induce irregular bearing for some species. However, the understanding of plant responses to temperature stress lags behind other biotic and abiotic stresses probably due to the complex response at the molecular, cellular, and organismal level. Temperature stress affects, indeed, many developmental processes during the plant's life cycle. However, the reproductive stage, the outcome of which represents the economic value for many cultivated plants, is especially vulnerable. Here the effect of low and high temperature stresses during the flowering phase is reviewed in flowering plants in an attempt to unravel sensitive stages that are behind irregular cropping. The review presents detailed findings from 33 previously published reports spanning 19 different flowering plant species. Both the male and female organs of the flower are especially sensitive to temperature fluctuations both during their development before pollination and during the post-pollination stage. The effect of temperature stress is, however, obscured by the complex male–female interaction superimposed on the individual behavior of each organ. Interestingly, a review of the literature on this topic shows that genetic variation does exist in reproductive behavior under temperature fluctuations. This genetic diversity must be preserved and characterized in further detail to understand how plants naturally cope with changing environmental conditions, which will, undoubtedly, help us to design better strategies to face current and future challenging temperature fluctuations.

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1. Introduction

Temperature stress affects different plant developmental and physiological processes (Hall, 2001) and is considered one of the major constrains to plant adaptation, especially when it coincides with critical stages of plant development (McWilliam, 1980). One of the main objectives in plant domestication has been to spread cultivated plants along a larger geographical range and significant efforts have been dedicated to increase plant tolerance/avoidance to temperature fluctuations (Hall, 2001). Furthermore, studies on temperature tolerance in different crops are needed, now more than ever before, for two major reasons. First, although technological progress during the last century has pushed yields close to their

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maximum potential in many species, it has barely kept pace with population growth, which is expected to raise up by 2–4 billions by 2050 (Cohen, 2003; Trewavas, 2002). However, increasing available farmlands is hardly feasible without plowing up virgin lands and forests and, thus, deteriorating further the already threatened natural habitats and biodiversity (Trewavas, 2002). Second, the recent linear trend of 0.74 °C increase in the average global near-surface temperature registered between 1906 and 2005 (Solomon et al., 2007) seems to support the fact that, indeed, we are facing an unequivocal global warming which may represent another challenge to plant productivity and geographic distribution (Hedhly et al., 2009).

For many cultivated plant species the economic value lies in the outcome of the sexual phase, resulting in the seed and/or the fruit. It is known that temperature variation outside the range of species tolerance during flowering can jeopardize fruit and seed set. Both in cultivated and wild plant species low and high temperatures have been shown to make fruit set erratic if not null (Section 2). The reported underlying causes of such effects are, however, very diverse. This is because, first, both the timing and extension of temperature stress – either natural or experimental – are remarkably variable. Second, because species, and even varieties/landraces/ecotypes within species, differ in their sensitivity to temperature and/or in the particular stage that is the most sensitive.

This review examines the implications of temperature stress during the flowering phase on fruit and seed set in cultivated and wild plant species. It shows that (i) both low and high temperature stresses during the flowering phase could largely explain erratic and reduced fruit and seed set; (ii) the three genetically different elements that are present and interact within a flower, the sporophyte – pistil tissues – and the two gametophytes – pollen and embryo sac, are specially sensitive to temperature stress; and (iii) genetic variation that likely reflect adaptation to temperature stress does exist at both the interspecific and intraspecific levels.

2. Low and high temperature stresses at flowering result in erratic fruit/seed set

Many cultivated and wild plant species within different climatic regions worldwide perform poorly and display erratic fruit and seed set when subjected during their flowering phase to high and low temperatures beyond their optimum needs. For example, in temperate fruit trees, a substantial reduction in fruit set has been shown in apricot (*Prunus armeniaca* L.) after an increase in the average daily temperature as low as 3 °C during the week preceding anthesis (Rodrigo and Herrero, 2002), or in sweet cherry (*Prunus avium* L.) during the first two weeks following anthesis (Hedhly et al., 2007). Similarly, results in peach (*Prunus persica* L. Batsch), show that a two month exposure to different constant temperatures in growth chambers, starting 1 month before anthesis, resulted in very low fruit set above 25 °C (Kozai et al., 2004). In pear (*Pyrus communis* L.), Mellenthin et al. (1972) found a linear relationship between mean maximum temperatures registered during the first 10 days following anthesis and fruit set.

Likewise, tropical fruit trees are usually sensitive, during their flowering phase, to temperature fluctuations in subtropical and temperate regions, a characteristic that limits the extension of their cultivation range. Mango (*Mangifera indica* L.) has been shown to be prone to recurrently erratic fruit set with an increased proportion of stenocarpic fruits when temperature falls below 10 °C during flowering (Sukhvibul et al., 2005). Cherimoya (*Annona cherimola* Mill.), native to the tropical highlands of the Andes, usually displays lower fruit set in tropical lowlands and in temperate regions. An increase in temperature from 20 °C to 30 °C during two consecutive years reduced substantially fruit set and increased the number of malformed fruits (Higuchi et al., 1998). In avocado (*Persea americana* L.), higher fruit set has been obtained in the range of 20–25 °C; temperatures outside this range negatively affected fruit set either by impairing fertilization (17 °C) or by abscission of unopened flowers (33 °C) (Sedgley, 1977).

Annual crops also suffer from both low and high temperature stresses occurring during the flowering phase. Due to their economic importance, the effect of temperature stress on the reproductive process has been extensively studied in cereals (see Barnabás et al., 2008; Thakur et al., 2010 for extensive reviews on the subject). Special mention must be given to the work done in rice (*Oryza sativa* L.), initiated in the 1970s by Japanese researchers (Nishiyama, 1984; Satake and Hayase, 1970) and later confirmed by many authors (e.g. Jagadish et al., 2007; Mamun et al., 2006; Prasad et al., 2006), relating chilling and heat stress during booting (early gametophyte development) and flowering to higher spikelet sterility. Similarly, the effect of high temperatures during flowering in tomato (*Solanum lycopersicum* L.) has also been studied in detail, and not only extreme high temperatures, but even a mild increase in temperature during a short spell coincident with some flowering stages have been shown to affect negatively fruit set (Abdulbaki and Stommel, 1995; Sato et al., 2002). Bell pepper (*Capsicum annuum* L.) has been reported to be equally sensitive to high temperature stress during flowering (Erickson and Markhart, 2002). Rapeseed, flax, groundnut, common bean, cowpea and *Trifolium repens* are some of the many other species, with economic importance in some regions of the world, that are sensitive to temperature fluctuations during flowering resulting in lower fruit and seed set (refer to Supplementary Table 1 for further details on these and other species).

Although scarcer effort has been dedicated to the effect of temperature stress on seed and fruit set in natural populations, sensitivity to temperature stress during flowering has also been shown for some species (e.g. *Primula* sp.: (McKee and Richards, 1998); *Plantago lanceolata*: (Lacey and Herr, 2000)). In summary, temperature fluctuations outside the range of species tolerance occurring during the flowering phase seem to alter seed and fruit set in different species and in diverse climatic regions worldwide. In the next 3 sections I will try to answer two main questions, namely; (in Section 3) why is flowering so sensitive to temperature stress? and (in Sections 4 and 5) what are the specific reproductive processes or components that underlie such sensitivity?

3. Flowering stage sensitivity to temperature fluctuations

Temperature stress during flowering affects yield. First, because flowers are the organs that develop into fruits, and any biotic or abiotic pressure that affects their likelihood to set seeds and/or fruits necessarily affects yield. Second, some target oriented works carried out to unveil temperature sensitive stages during plant development have found recurrently that the reproductive process is the most sensitive stage to temperature stress showing a narrow tolerance threshold to temperature fluctuations (Porter and Semenov, 2005). For simplicity, these studies can be categorized into: (i) those applying the stress at different developmental stages, including vegetative growth, and analyzing the effect on both vegetative and reproductive development, and (ii) those confining the stress to some specific stages of reproductive development and searching for the determinant phase; examples from these two approaches are further detailed in Supplementary Table 1.

Within the first approach, subjecting wheat plants (*Triticum aestivum* L.) to a heat period of eight days during the double-ridge stage (25 °C) and/or during anthesis (35 °C) revealed that grain yield was only significantly reduced when treatments were applied at both stages or at anthesis alone (Wollenweber et al., 2003). Rice subjected to 34 °C (6 °C increase over the control) displayed higher leaf expansion and greater biomass, but grain yield decreased 10% for