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Effect of High Temperature on Reproductive Phase of Plants: A Review

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ABSTRACT

Climate change is a universal challenge that threatens the very existence of life on planet Earth. One of the most sensitive areas to climate change is agriculture. Climate change affects precipitation, cyclones, clouds, temperature, humidity, and CO_2 levels. All these factors affect plant productivity which poses another grave concern in feeding the ever-increasing population. The productivity in terms of crop yield is reduced due to a direct correlation between phenology and climate change. The reproductive organs of a plant and other parameters that define good fertility of a species are all affected by the increasing temperatures during their vegetative and reproductive phases of growth and development. Thus, this review is an attempt to understand the effect of climate change on the reproductive structures of plants and discuss the short-term and long-term adaptations in plants and agriculture as mitigation measures to combat the significant yield loss in developing countries.

INTRODUCTION

Climate change is a grave concern impacting the production of various crops worldwide. One of the important components of global climate change is an increase in the Earth's near-surface temperature. Unusually dry and hot climatic conditions have been linked with a lessening of several tree species around the world. Physiological stress associated with fluctuation in temperature poses a serious threat to biodiversity by causing alteration in reproductive processes and plant-pollinator associations (Talwar et al. 2015, Rawat 2015).

The process of sexual reproduction contributes a dominant role in the life-cycle of plants and it is prone to any turmoil in the environment (Müller et al. 2016). The yield of the crop is an important parameter for human survival. Stakeholders are using various methods and techniques based from satellite remote sensing (Bamel et al. 2022) to mathematical modeling (Rani et al. 2022) to forecast the yield of crops. Agronomists use all available information related to nutrient, irrigation, and climatic requirement for their crops to enhance productivity. Seed production depends on vegetative as well as reproductive development. During the transition from the vegetative to a reproductive state of a plant, the environmental conditions usually affect photosynthetic efficiency, development of canopy, interception of solar radiation, and initiation of fruiting. An increase in the temperature of just a few degrees can considerably affect the yield of the crop (Thuzar et al. 2010).

Several morphological, physiological, developmental, and molecular responses of the reproductive structures may vary under climatic stresses (Gray & Brady 2016). The shift in the flowering period is a result of temperature variation and inconsistency in precipitation. The reproductive period and the reproductive structures are more susceptible to temperature stress than the development of vegetative organs, which eventually affect the crop yield (Snider & Oosterhuis 2011). According to Foolad (2005), high temperature negatively affects the various reproductive processes such as pollen viability, germination of pollen grains, growth of pollen tube, positions of stigma and style, pollen-pistil interaction, fertilization, and post-fertilization processes, such as the growth of the pro-embryo, endosperm and zygote.

Every crop shows optimal vegetative and reproductive growth at its own threshold temperature (Hatfield et al. 2011, Zinn et al. 2010). When the temperature overshoots the threshold range of crops, its vegetative and reproductive growth such as flowering, fruit set, fruit ripening, and seed germination are gravely affected and have an economic impact on agriculture (Christensen & Christensen 2007). The progamic phase, which extends from pollination to fertilization, is one of the most crucial phases and is extremely vulnerable to high temperatures (Hebbar et al. 2020).

To fulfill the food demand of the increasing population, it is mandatory to elucidate and strengthen the mechanisms that regulate pollination, leading to enhanced yield. The authors attempt to search the available literature that highlights the significance of temperature stability for the sustenance of the usual reproductive systems of plants and how the slightest variation from the optimum affects the process. Suitable studies were screened to understand the stress impact on different plant organs that are important for the reproductive phase and adaptations of plants, if any, to combat or overcome it and complete their life cycle normally. This in-depth analysis led the investigators to give a comprehensive perspective and address the knowledge gaps by defining the future scope of research in the study area which is one of the most important concerns of humanity in today's changing environmental scenario. If change is inevitable then mankind has the challenge to slow it by curtailing the responsible factors or else find alternatives that can sustain life amid the changes.

EFFECT ON PRE-ZYGOTIC REPRODUCTIVE PHASE

Flower

Flower and its various constituent parts are very sensitive to the temperature both structurally and functionally as was observed in rice (Takeoka et al. 1991) and *Brassica* (Morrison & Stewart 2002). Depending upon the plant species temperature stress shifts the flowering either way. Most often higher than optimum temperatures are perceived as stress by the plant and in response, the flowering is preponed. In cowpea, the higher temperature at night is more detrimental in comparison to higher day temperature, which results in enhanced floral abscission (Mutters & Hall 1992).

Cubillos and Hughes (2016) investigated the impacts of elevated carbon-di-oxide on the floral traits of the three economically important crops tomato, pepper, and zucchini. The elevated CO_2 treatment did not affect flower longevity in any of these three species, it did not affect flowering in tomatoes, but less number of flowers were produced in pepper, whereas in zucchini more male flowers than female flowers were developed. At elevated CO_2, fewer pollen grains and reduced nectar secretion have been observed in zucchini whereas no such difference was observed in tomato.

Pollen

Various studies have revealed that the growth and development of male gametophytes are extremely sensitive to heat (Hedhly et al. 2009, Hedhly 2011, Zinn et al. 2010). Increased temperature affects the pollen grains in terms of number and viability. The viability of the pollen grains is a prerequisite for successful sexual plant reproduction. The quality of pollen grains is assessed on their viability over a period after dehiscence. The duration of pollen viability affects the reproductive success of a species. Due to the temperature stress collapse, desiccated, empty, and small-sized pollen grains with reduced viability are formed in chickpeas (Devasirvatham et al. 2013). Pollen viability is affected by heat stress in several plants such as common bean (Gross & Kigel 1994, Prasad et al. 2003), cowpea (Warrag & Hall 1984), peanut (Boote et al. 2005), cotton (Song et al. 2015), flax (Cross et al. 2003), pepper (Erickson & Markhart 2002), rice (Endo et al. 2009), and tomato (Pressman et al. 2002).

Reduced pollen vigor has been reported in *Brassica* and *Petunia* when pollen grains were exposed to 45-60^{o}C for 12 h (Rao et al. 1992). In *Glycine max*, when plants were exposed to 38^{o}C during the day, the number of pollen grains was reduced (30-50%) and when exposed to 30^{o}C at night, the viability of the pollen grains was also decreased (Koti et al. 2005). Similarly, in *Arachis hypogea* when kept under elevated temperature (44^{o}C), the viability of the pollen grains was reduced (Prasad et al. 2003).

Temperature above 35^{o}C caused the development of sterile pollen grains and thus affected the pollination and fertilization of rice. Higher temperatures inhibited the germinated pollen tubes to reach the embryo sac, affecting the fertility of the spikelet and crop yield (Shi et al. 2018). In cotton, exposure to 39°C, reduced pollen germination to 40% (Burke et al. 2004). Similarly, pollen viability and pollen tube elongation were reduced above 32°C and 29°C respectively (Kakani et al. 2005). In different potato varieties, pollen germination and crop yield were decreased between 30 to 70%, when the pollen grains were exposed to 30°C for up to 30 minutes although the seed set was less affected (Pallais et al. 1988).

In sorghum, the pollen grains showed the enhanced accumulation of reactive oxygen species (ROS) when the plants were exposed to high temperatures. The pollen membrane was damaged and pollen grains were small and deformed which eventually resulted in a reduced seed set (Djanaguiraman et al. 2018). Similarly, heat stress resulted in pollen sterility, lowering the seed set and crop yield in maize (Wang et al. 2019), kidney bean (Prasad et al. 2003), and chickpea (Kaushal et al. 2013).

Pistil

During the pollination process, pollen grains fall on the receptive stigma, and in response to the stigmatic fluid pollen grains adhere to the surface and it is soon followed by hydration and germination. By penetrating the transmitting tissue of style through stigma pollen tube reach the ovule and discharges all its contents into the embryo sac to facilitate fertilization (Hiscock & Allen 2008, Losada & Herrero 2012). The compatibility between pollen and stigma is also required for effective fertilization. If the pollen grain is compatible, all post-pollination events (fertilization, fruit, and seed set) proceed normally, but if the pollen is incompatible, the pistil effectively arrests one or more of the post-pollination events, thus preventing fertilization. The most distinct response of the stigma to incompatible pollen is the development of a callose plug which appears at the tip of the pollen tube, thereby preventing its further growth (Bhojwani et al. 2015).

The stigmatic receptivity and ovule degeneration are important parameters that control the interaction of male and female reproductive phases and have significant consequences on pollination. These processes are temperature-dependent (Cerović et al. 2000, Lora et al. 2011). Elevated temperature reduced the period of stigma receptivity, ovule life span, and style abscission from the ovary, whereas low-temperature exposure had opposite effects (Montalt et al. 2019, Estornell et al. 2016). Heat stress-induced stigma enlargement because of elongation of stigmatic papillae and reduce the adherence of pollen grains to stigma (Katano et al. 2020). It also shortened the filament length. These observations indicated that the decrease in pollen attachment to stigma might be partially due to short stamen which might increase the distance between stigma and anthers.

The receptivity of the stigma was strongly controlled by the elevated temperature and it significantly decreased the pollen germination as well as the number of pollen tubes growing on the stigma in citrus (Montalt et al. 2019). High temperature significantly influenced the processes of ovule degeneration and the style of abscission. In canola, high temperature also shortened the period of stigma-nectar secretion, affecting pollinator-based pollination efficiency (Chabert et al. 2018). Wang et al. (2021) studied the effects of heat stress on pistils and concluded that high temperatures affect the development of female gametophyte, pollen-pistil interactions, fertilization, and post-zygotic development and suggest more molecular studies to understand the regulatory mechanism involved in the female gametophyte development.

Pollen-Pistil Interaction

Pollen-pistil interaction involves a series of reactions between the male gametophyte and sporophytic tissue of the stigma and style. These interactions result in the generation of appropriate physical and chemical signals which elicit the required responses in pollen or pistil. Pollination, pollen adhesion, pollen hydration, pollen germination, growth of pollen on the stigma, growth of pollen tube through the style, and entry of pollen tube into the ovule are sequential major events of this interaction. Any deviation prevents fertilization and as a result fruit and seed set. This is the most delicate period in the life span of the plants as various processes are involved during this short period of time (Hedhly et al. 2009, Zinn et al. 2010).

Several works have shown the impact of high temperature during the initial phases of pollen-pistil interaction. High temperature has been shown to affect stigmatic receptivity in peach (Carpenedo et al. 2020), cherimoya (Lora et al. 2011), ovule degeneration in plum, sweet, and sour cherry cultivars (Beppu et al. 2001, Cerovićet al. 2000, Postweiler et al. 1985). In coconut, high temperature (33^{o}C) induced the nectar secretion before the stigma became receptive and at the time of pollination, the stigma was dry. This significantly affected the pollination, fertilization, and seed set (Hebbar et al. 2020).

BIOCHEMICAL AND MOLECULAR CHANGES ASSOCIATED WITH HIGH TEMPERATURE

Physiological and biochemical processes such as oxygen requirement during seed imbibition are severely affected by elevated temperature (Nascimento et al. 2008). Saini (1997) reported that malfunctioning of gametophytic development is also due to the stress-induced reduction in sugar delivery to reproductive tissues. Later, Snider et al. (2009) showed a significant decline in the amount of soluble carbohydrates and ATP content in the pistil of cotton when the plant was exposed (38^{o}C/20^{o}C) for a week before flowering, resulting in a reduction in the number of ovules and fertilization efficiency. Similarly, Li et al. (2015) observed that sugar starvation is the major cause of the failure of fertilization in rice because of the high temperature. It is due to the presence of acid invertase enzymes as invertase hydrolyzes sucrose into hexose which supports the pollen tube growth (Goetz et al. 2017). Under heat stress, the activity of the invertase enzyme was significantly decreased and thus restricted the hexose sugar supply. Similarly, the pistils of cotton flowers also showed less amount of carbohydrate reserves (particularly sucrose) and ATP production under the effect of moderately high temperatures, and thus there is a decline in photosynthesis because of the heat stress (Snider et al. 2011). Providing the exogenous acid invertase increased the amount of carbohydrates content as well as increased the spikelet fertility in Rice (Jiang et al. 2020). The interaction between sugars and hormones is also indicated by Kumar et al. (2021) whereas Jagadish et al. (2021) have reviewed the carbon dynamics and suggested not to draw a general conclusion about the role of sugars in crop reproduction.

FUTURE SCOPE AND PERSPECTIVE

Though the rise in temperatures has detrimental effects on almost all physiological and developmental processes, it becomes an even more serious concern if the impacted stage is reproduction. The ultimate toll is taken by the quality (nutrient content) and quantity (yield) of the products like in food crops. Since plants respond to multiple abiotic factors, a multidisciplinary understanding needs to be developed keeping in mind the interaction of different factors like the fluctuating temperature, and increasing CO_2 and nitrogen levels in the atmosphere.

'Omics' approach, targeting heat stress in plants in general and crop plants in specific, is the need of the hour. To mitigate the impact of rising temperatures new stress-tolerant species should be identified. The correlation between the genotypic and phenotypic studies will help in screening the appropriate genotype that can thrive well in the changing environment. The varieties may be selected from the existing gene pool based on their flexibility in flowering and anthesis time or their morphological feature that confer their tolerance to heat stress. The potential stress-tolerant germplasm may then be screened for specific genes that confer better adaptability to the changing scenario. Susceptible genotypes may be targeted for improvement by introducing the tolerant traits using the techniques of genetic engineering.

More work at the molecular level may elucidate the effect of the increase in air temperature on the floral tissue temperature. Extensive studies focusing on membrane fluidity, cytoskeleton, chromatin structural modifications, changes in enzyme activities, and signaling cascades are necessary. The information about changes in the plant and floral transcriptome due to high-temperature stress will pave way for focused adaptation and mitigation strategies. Another approach may be to use epigenetics to generate modified resilient genotypes with potential tolerance to the environmental stresses that are a threat to their normal growth and development. A better understanding of heat stress-induced biomolecules like osmoprotectants, heat shock proteins, free radical scavengers, membrane ionic transporters, and transcription factors may come to the rescue of plant biologists to develop effective mitigation strategies.

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