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CLIMATE CHANGE: MOLECULAR ADAPTATION STRATEGIES IN CEREALS AND FORAGE CROPS–A REVIEW

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SUMMARY

Owing to various anthropogenic activities, atmospheric CO_2 concentration continues to rise and in turn enhance average global temperature causing climate warming. Elevated atmospheric CO_2, enhances Ribulose1,5-bisphosphate carboxylase (photosynthesis) activity and reduces Ribulose1,5-bisphosphate oxygenase activity (photorespiration) in C_3 plants. Annual mean temperature has increased about 0.4 ºC over the last century. Increased temperature affects crop yield, as it shortens plant growth and developmental phases. With continued increase in population, crop yields must also increase to meet the future requirements of food and fodder. This article reviews the impact of elevated CO_2 and temperature on physiological and biochemical responses of cereals and forage crops and also the molecular adaptation strategies for the development of climate-resilient crops for sustainable food and fodder security.

Key words : Climate change, molecular adaptation mechanism, cereals, forage crops

The climate emergency owing to the increased emission of greenhouse gases and other anthropogenic activities is posing risk to sustainable food and fodder security worldwide. Atmospheric CO_2 concentration has elevated from approximately 280 ppm in the pre-industrial era to 400 ppm presently, due to excessive use of fossil fuels and other activities including deforestation. The average global temperature increased by about 1°C since 1880 (Crous, 2019). Atmospheric CO_2 concentrations continue to rise and is predicted to reach approximately 550 ppm by 2050 and 700 ppm by the end of this century (Becklin *et al.,* 2016). This would further enhance warming with average global temperature predicted to be increased by 1.1-4.8 °C depending on the magnitude of the emissions of greenhouse gases (IPCC, 2014; Borland 2015). Further, high latitudes may experience severe warming, about 10°C increase in temperature, by the year 2100, on the other hand, the tropics may experience comparatively smaller temperature increases of about 3-4°C (Ciais *et al.,* 2013). Furthermore, climate warming is expected to cause changes in the precipitation patterns leading to extremes in dry and wet spells (Medvigy and Beaulieu, 2012).

Climate warming is predicted to have enormous impact on the Earth's flora and fauna. The continued rise in global CO_2 levels and the climate change phenomenon thereupon will have huge influence on ecosystems and other natural resources. Agriculture and allied activities are predicted to be most affected as climate warming will have direct as well as indirect effect on crop production, soil microbes, livestock and pests. The predicted extreme changes in the climate may detrimentally affect crop productivity. Furthermore, human population is ever growing and have been predicted to reach 9 billion by

2050 necessitating approximately 70 % enhancement in crop production (FAOSTAT, 2017; Bhat *et al.*, 2020). Therefore, ensuring food, fodder and nutritional security and development of crop varieties with high nutritional and yield potential and are adaptable to the challenging future climate scenario is of prime importance.

Cereals including wheat, rice, maize, barley and millets serve as staple crops and are among the major food grains produced across the globe. The pros and cons of climate change on cereal crops will have a tremendous influence on food security as they are among the staple foods. There is a high demand for cereal and forage yield and seed production at the present and in future as well. A major challenge ahead for those involved in the seed industry, therefore, is to provide cultivars that can maximize future crop yields under the changing climate (Ainsworth *et al*., 2008b; Bruins 2009; Ceccarelli *et al*., 2010). Climate resilient crops such as leguminous forages : berseem, cowpea, centro, clitoria and siratro (Dheeravathu *et al*., 2017a and b, Dheeravathu *et al*., 2021a, Dheeravathu *et al*., 2021c, Dheeravathu *et al*., 2022), grasses: guinea grass, bajra-Napier hybrids and a tri-specific hybrid, dinanath grass (Dheeravathu *et al*., 2018, Singh *et al*., 2020, Dheeravathu *et al*., 2021b, Singh *et al*., 2021, Antony *et al*., 2021, Dheeravathu *et al*., 2022), cereal forage : oat (Dheeravathu *et al*., 2022), and forage millets: sorghum, pearl millet (Singh *et al.,* 2010) have been proven to be climate smart. Considering the effect of elevated CO_2 and temperature on forage growth, yield and productivity, identification of physiological and biochemical changes mechanisms and molecular adaptation strategies in cereal and forage crop varieties/genotypes/lines could play a major role in sustaining food, forage and livestock production and will be helpful in future breeding programs. In this review, the impact of elevated CO_2 and temperature on cereal and forage crops and also the various strategies adaptation to tackle the detrimental effects for sustainable agriculture and food security are discussed.

Effect of rising CO_2 and elevated temperature on cereals and forage crops

Rising CO_2 levels directly impact plant metabolism owing to its role in the photosynthetic process and hence are expected to evoke profound physiological and biochemical alterations in plants. Increased CO_2 indirectly impacts plant performance through its effect on temperature and water stress as well as by directly affecting the plant metabolism through its role in photosynthesis (Kanwal *et al*., 2014; Abebe *et al*., 2016). Under elevated atmospheric CO_2, Ribulose1,5-bisphosphate carboxylase/oxygenase (Rubisco), a key enzyme of photosynthetic pathway, can better bind to CO_2, enabling enhanced carbon fixation. Thus, in general, elevated CO_2 levels stimulate photosynthesis initially and also simultaneously supress oxygenation that causes photorespiration (Bowes 1991). The enhancement of photosynthetic process due to elevated CO_2 is profound only when the internal CO_2 concentration is low; *i.e.*, when the rate of photosynthesis is limited by rubisco carboxylation. With further increase in the internal CO_2 concentration, the photosynthetic process becomes less dependent of CO_2 concentration (as it already saturated) and is limited by the ability to regenerate RuBP. Thus, increase in the CO_2 levels in C_3 plants (including rice and wheat among others) results in net stimulation of photosynthesis initially and hence increased biomass accumulation (Ainsworth and Long, 2005). Improved tillering and shoot biomass have been reported in wheat under increased CO_2 levels (Bourgault et al., 2013). But with further increase in CO_2 concentration for longer periods, stimulation of photosynthesis is not maintained due to acclimation process (Long *et al*., 2004). On the other hand, plants with C_4 photosynthetic pathway (including maize, sorghum, pearl millet) devise a different primary carboxylase, phosphoenolpyruvate carboxylase (PEP carboxylase). PEP carboxylase assimilates CO_2, fixes it as oxaloacetate in the mesophyll cells which is then decarboxylated in the bundle sheath cells. Thus, in C_4 plants, CO_2 is delivered to the bundle sheath cell rubisco in higher concentrations enhancing photosynthetic efficiency and inhibiting photorespiration (Leakey, 2009; Kant *et al*., 2012). Rise in atmospheric CO_2 levels will lead to a rise in intracellular CO_2 concentration in C_4 plants; however, it may not have profound effect on carbon fixation and biomass production as they already are nearly photosynthetically saturated (Ainsworth and Long, 2005; Kant *et al*., 2012). Free-air CO_2 enrichment studies revealed enhanced yield in C_3 plants under elevated CO_2 without any stress on the other hand, productivity C_4 plants were not increased except under drought stress (reviewed in Ainsworth and long, 2020). Nevertheless, significant enhancement in yield and biomass production of C_4 nutri cereal, foxtail millet was observed under elevated CO_2 levels as determined by open-top chamber studies (Gong *et al*., 2021). For other growth and/yield related characteristics, plant responses to elevated CO_2 levels vary considerably (Kadam *et al*., 2015).

Further, rise in CO_2 levels considerably lowers stomatal conductance and in general improves the water use efficiency (WUE), as have been reported in wheat (Li *et al.,* 2004). Decreases up to 20% stomatal conductance have been reported in the Free Air CO_2 Enrichment (FACE) owing to rise in CO_2 levels, while, in some studies (Pathare *et al.,* 2017), lowering of stomatal conductance have not been observed. Nevertheless, the decreased stomatal conductance leads to increased resistance in CO_2 diffusion and thus offsets rubisco carboxylation rates. Lowered stomatal conductance enhances soil water savings, enabling to compensate the expected future higher evaporative demand thus promoting crop productivity. Furthermore, reduced stomatal conductance and the lowered transpiration rates results in elevated leaf temperature (Madan *et al*., 2012) which in turn causes greater leaf to air vapour pressure difference (VPD), a driving force for transpiration. This counterbalances the water savings from decreased stomatal conductance under elevated CO_2 and hence the overall transpiration rate under elevated CO_2 is only minimum as compared to ambient CO_2.

Effect of elevated CO_2 on flowering time shows that there exist slight advancements in flowering time in many C_3 plants including cereals *viz*. rice and barley (Craufurd and wheeler, 2009). Also, higher spikelet sterility was observed in rice and sorghum owing to enhanced CO_2 during anthesis (Matsui *et al*., 1997). Further, elevated CO_2 induced decrease in grain protein and micronutrients have been reported in some crops; for instance, Li *et al*. (2019) found a decrease in grain Ca and K content in wheat. More recently, Gong *et al.* (2021) reported that elevated CO_2 decreased Fe content of foxtail millet grains while it enhanced accumulation of P in the grains. As temperature plays critical role in all the processes associated with plant growth and development, elevated temperature would have profound impact on crop productivity. Increased temperature affects crop yield, as it shortens plant growth and developmental phases through alterations in the rate and timing of physiological processes (Ahad and Reshi, 2015, Dheeravathu *et al*., 2022). Enhanced leaf temperatures result in increased stimulation of photorespiration owing to the shift in specificity of Rubsico for O_2 at higher temperatures and also enhanced solubility of O_2 as compared to CO_2 in turn leading to higher availability of O_2.

Elevated temperature beyond the optimum temperature for photosynthesis would have negative effect on plant growth and yield. The temperature optimum of photosynthesis may vary among plant species with those adapted to hotter climates having higher values as compared to those adapted to colder region (Sage and Kubien, 2007). Also, C_4 plants possess a higher optimum temperature as compared to C_3 plants (Crafts-Brander and Salvucci, 2002). Decline in photosynthesis at elevated temperatures (*i.e*., temperatures above the thermal optimum of assimilation) can be explained in terms of heat labile nature of enzymes including rubisco activase, the enzyme that catalyses removal of inhibitory molecules from the catalytic site of rubisco and the reduction in the electron transport at elevated temperatures (Dusenge *et al.,* 2019). Lower shoot biomass accumulation during vegetative phase owing to decreased photoassimilate production caused by heat stress induced on photosynthetic machinery have been reported in maize (Sinasawat *et al.,* 2004). Further, rise in air temperature causes an increase in the air saturation vapour pressure leading to an increased vapour pressure deficit between air and leaf which in turn decrease water-use efficiency of plants (Ahad and Reshi, 2015). High temperature stress adversely affects reproductive stages of crop development in cereals often causing fewer spikelets/grains and reduced sink size (Kadam *et al.,* 2014). Elevated temperatures above the optimal range adversely affects pollination process; heat stress induced floral abnormalities including pistil hyperplasia adversely affects reproduction in rice (Takekova *et al*., 1991). Reduced pollen viability, poor pollen germination, anther indehiscence induced by heat stress have been reported in rice (Jagadish *et al.,* 2007; Rang *et al.,* 2011). High temperature stress during pre-anthesis stage decreases pollen or ovule viability and/or stigma receptivity (Prasad *et al.,* 2008, Nguyen *et al.,* 2013, Djanaguiraman *et al.,* 2014, Prasad and Djanaguiraman, 2014), causes reproductive structure abnormalities (Prasad and Djanaguiraman, 2014) and oxidative damage, resulting in pollen sterility and decreased seed-set (Djanaguiraman *et al.,* 2014). High temperature stress at the time of anthesis can decrease floret fertility even when the pollen is viable (Prasad and Djanaguiraman, 2014). The other negative impacts of elevated temperatures in cereal crops include drastic reduction in grain yield. Low grain weight in cereals including rice and wheat associated with poor assimilate remobilization and poor grain filling due to increased temperature have been observed (Kadam *et* *al.,* 2014). Furthermore, heat stress impacts antioxidant enzymes; for instance, negative influence of heat stress on antioxidant enzymes of maize have been reported by Gong *et al.* (1997).

Climate change: Application of genomics and molecular breeding approaches in the molecular adaptation mechanism in cereals and forage crops

The phenomenon of global climate change, with its wide spread impact on agricultural productivity, continues to be one of the major environmental challenges of twenty-first century. With the future predictions of extreme weather events, owing to high carbon emissions, it is implicit that better strategies to adapt to the changing climate scenario are needed. Cultural methods *viz*. alterations in the crop planting and harvesting time, changes in the cropping schemes, crop rotation and adoption of crops with shorter life cycle *etc* are devised by farmers. With the prediction of extreme heat in the coming years, breeding efforts to develop cultivars that are adapted to heat stress, drought and other abiotic stress would enable sustainable crop improvement and productivity.

Conventional breeding approaches are valuable tools in developing stress-resistant crop cultivars; however, more efficient and rapid strategies are needed to address present climate change and food insecurity challenges. Crop improvement strategies are based upon genetic diversity of crop species and the development of crop cultivars with improved adaptation to various abiotic stress would be beneficial in mitigating the effects of climate change. Land races of crops serve as important source of genetic diversity as they display adaptation to agro-climatic conditions in which they survive and are hence excellent tools for crop improvement programs (Lopes *et al*., 2015). Evaluation of drought response in 105 land races of pearl millet on a wide range of environmental conditions enabled the identification of 15 land races with high degree of tolerance to drought that can be used in the development of drought tolerant cultivars (Yadav *et al*., 2003). With the advancement in molecular biology tools, genotype-based strategies started gaining importance. Advanced tools employed for the development of improved crop cultivars include genetic engineering (GE)-based strategies and molecular breeding approaches (Kole *et al*., 2015). GE based strategies allow transfer of gene (s) of interest to crop plants for generating desired phenotype. This technique of transgenic plant development has been widely employed to develop crops that are resistant to a number of abiotic stresses. For instance, transgenic rice, over expressing *OsDREB2A* under a stress inducible promoter from *Arabidopsis* with improved resistance to salinity and drought have been developed (Mallikarjuna *et al*., 2011). Further, transgenics enabled better understanding of various aspects of plant development including response to stresses. Nevertheless, the integration of foreign genes into edible crops are controversial in many countries (Kole *et al*., 2015; Jaganathan *et al*., 2018).

Molecular breeding approaches are promising as they enable expansion of the size of breeding program, in turn enhancing selection intensity (Yuan *et al.,* 2019). DNA markers or molecular markers including RFLP, AFLP, SSRs, SNPs *etc* have been widely employed to identify QTLs for understanding the underlying mechanism of stress adaptation in crops including cereals and thereby contributing to crop improvement under stress condition. The marker-assisted selection (MAS) for various crop improvement strategies including those targeting abiotic stress tolerance have accelerated breeding strategies with reduced need for extensive field selection. Linkage mapping to identify markers associated with traits of interest have been widely employed in several crops including cereals (Kulwal *et al*., 2011). Yadav *et al.* (2002) performed QTL mapping to dissect traits determining grain and stover yield under terminal drought tolerance in pearl millet. However, attempts to improve complex traits by QTL -associated markers displayed limited success owing to the low resolution in the identification of markers associated with small effect QTLs (Kulwal *et al*., 2011) and also difficulty of finding same QTLs across different environments (Crossa *et al*., 2017). Hence, association mapping with its increased mapping resolution and greater allele number is being widely employed for dissecting complex traits in crops.

The recent advances in genomics and allied areas, allowed molecular breeding approaches to further comprehensively characterize allelic diversity underlying agronomic traits of interest including those confer abiotic stress tolerance and their application in the development of novel cultivars with improved climate resilience. Advances in NGS offers cost effective genotyping assays, large numbers of numerous genomic resources including genome-wide molecular markers *viz*. SNPs and insertion-deletions (InDels) *etc* have been developed for crops which are serving as promising tools for genomics assisted breeding (Kole *et al*., 2015). Owing to their high density, SNPs are among the markers of choice for QTL mapping. Recently, the rapid and robust technique of Genotyping by sequencing (GBS) have been widely employed for the generation of genome wide SNPs (Poland and Rife, 2012). High-density linkage map construction and QTL analysis in maize, wheat, barley and oats were made possible through GBS (Poland *et al*., 2012; Huang *et al*., 2014). GBS also enabled the identification of alleles or genes responsible for the trait of interest in cereal crops including rice for seedling salinity stress tolerance (De Leon *et al*., 2016), pearl millet for drought tolerance (Debieu *et al*., 2018). These molecular markers are widely being used to assess genetic diversity, population structure and also to dissect genomic regions associated traits of interest through genome-wide association study (GWAS). GWAS is a powerful tool widely employed for the detection of genomic regions associated with any given trait and determination of statistical association between genetic polymorphisms including SNPs and trait variations in large germplasm collections. GWAS have been employed for the identification of candidate genes associated with agronomic traits including grain yield and the secondary traits under well-watered and drought stress conditions in maize (Xue *et al*., 2013; Thirunavukkarasu *et al*., 2014). Also, through GWAS, 365 single nucleotide polymorphisms (SNPs) associated with drought-related traits in maize was identified (Li *et al.,* 2016).

Furthermore, the high throughput genotyping and phenotyping techniques enables the employment of genomic selection approach. Genomic selection is a promising tool that enables to improve complex traits by capturing both major small effect QTLs with high density genome-wide marker coverage. Genomic selection increases the genetic gain per selection thus enhancing efficiency of breeding programs and is considered as an excellent alternative to MAS and other strategies (Srivastava *et al*., 2020). Genomic selection studies have been employed in the cereal crops including wheat, maize (Beyene *et al*., 2015; Shikha *et al*., 2017) and pearl millet (Varshney *et al*., 2017). Also, more recently, genome editing has emerged as an important tool to manipulate crop genome for better crop performance under biotic and abiotic stress conditions (Kole *et al.,* 2015). This strategy utilizes sequence specific nucleases and is a promising alternative to conventional breeding and incorporation of foreign DNA under the current climate change scenario. Zinc finger nucleases (ZFNs), Engineered homing endonucleases/ meganucleases (EMNs), transcription activator-like effector nucleases (TALENs) and clustered regularly interspaced short palindromic repeats/CRISPR-associated 9 (CRISPR/Cas9) are among the widely employed genome editing strategies. (Townsend *et al*., 2009; Silva *et al*., 2011; Cermak *et al*., 2011). The application of CRISPR/Cas tool for crop improvement under abiotic stresses have been employed in cereal plants including rice (Zhang *et al*., 2014; Shan *et al*., 2014) and maize (Shi *et al*., 2017).

CONCLUSION

The continued rise in global CO_2 levels and the climate change phenomenon thereupon will have huge influence on forage and cereal crop production and productivity. Increased temperature and drought stress incidences due to climate change reduce the quality and quantity of pollen grains resulting in low seed formation causing significant loss of forage and crop yield. Development of forage and crop adaptive traits with high nutritional and superior yield potential are recommended to meet the challenging future climate scenario to ensure food and nutritional security for the burgeoning global population. The advent of high throughput genotyping and phenotyping platforms with advanced genomic tools including the genome wide association studies, gene editing and genomic selection would enable better understanding of molecular mechanism of response to various stress and breeding of climate resilient cereal and forage crops. Knowledge on molecular mechanisms of plant adaptation to extreme temperatures/ heat stress, drought and other abiotic stresses are essential for effective management of unfavourable agro-ecologies in the wake of climate change. Despite great efforts in understanding the molecular mechanism associated with stress tolerance, more research is needed on molecular adaptation strategies on cereals and forage crops.

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