REVIEW ARTICLE Agricultural Reviews, Volume 45 Issue 2: 282-289 (June 2024)

Impact of Drought Stress on Grains Filling in Rice and its Management: A Review

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10.18805/ag.R-2369

ABSTRACT

Rice (*Oryza sativa* L.) is the world's single most important staple food source for over half of the world's population, whose demand is expected to increase as human population increases almost exponentially every year. There are different kinds of abiotic and biotic stresses that a rice plant endures. Among the different forms of environmental stresses, drought hampers the production of rice grains notably. The reality of climate change is so stark that more and more droughts are expected to be evident in the distant future. Water, being a requisite for rice cultivation, is gradually becoming a highly limited resource across the earth. In comparison to other cereal crops, rice is more sensitive to the soil water content. Decrease of soil water content or the unavailability of water triggers drought stress in rice. Therefore, the management of drought stress for the growth of rice plants is essential as even moderate stress during reproductive growth may result in a drastic reduction of grain yield. The distinct changes brought about by drought stress not only range from morphological to physiological changes but also from biochemical to molecular changes as well. A number of starch synthesis related enzymes like granule bound starch synthase I (GBSSI), soluble starch synthase IIa (SSIIa) play important role in grain filling, which are also affected by limited water under drought environment. Due to water scarcity, the rate of photosynthesis decreases, as a result of which dry matter accumulation decreases, which ultimately affects grain filling in rice. Drought causes delayed flowering as well as spikelet sterility, followed by low grain yield during harvesting. The prevalence of drought over longer periods causes reactive oxygen species to form within the rice plants which subsequently denatures proteins and nucleic acids. In many places where drought continues for longer periods, rice plants die resulting in huge loss of grain yields. The effective strategies that have been adopted involves- the development of stable drought tolerant rice varieties through plant breeding programs, the development of short duration rice cultivars which have short growing cycle and harvesting periods that may help the plant to escape drought, the development of rice plants having deep root system such that it can penetrate the soil to find the available moisture and water required for growth, as well as the development of transgenic drought tolerant rice plants which over express specific genes to withstand drought, are few of the effective management strategies that need special attention. Thus, it can be said that drought management for rice production is a crucial step towards food security and food production in the world. The present discussions will emphasize on the negative impact of drought in rice plants and also discuss possible key management practices that can address the existing and imminent drought related problems on rice plants.

Key words: Drought stress, GBSSI, Grain filling, Management, Reactive oxygen species, Yield loss.

Globally rice (*Oryza sativa* L.) is a major food crop, for production and consumption, comparable to other food crops like wheat (Todaka *et al.,* 2015). In 2013, rice cultivation was recorded from 124 countries around the world andproduction stood at 745 million tons (FAOSTAT). In a recent report (Dar *et al.*, 2020) the effect of drought on food security has been reviewed in Eastern India. Rice acts as a source of staple food for more than three billion people and served as a source of daily calorie intake (Khush, 2005). In rice, both reductions of growth and yield loss occurred due to the effect of drought (Basu *et al.*, 2016). In the farming of rice, water is a necessity which again is a highly limited resource (Wang *et al.,* 2012). Rice is very sensitive to drop in soil water content and also requires plenty of water for production compared to other cereal crops, normally 3,000 to 5,000 liters of water, are required for 1 kg of rice seeds production which is much higher than wheat and others crops (Singh *et al.,* 2002). Drought is the meteorological event, which implies the absence of rainfall for a period of time, long enough to cause moisture depletion in soil and water deficit with a decrease of water potential in plant tissues (Kramer, 1980). The rice ecosystem mostly suffers from drought at the time of flowering stage in both upland and lowland (Mishra and Chaturvedi, 2018). In rice, drought stress affects in various ways during rice production, which globally affects almost 23 million hectares of rice field, which are rain fed (Serraj *et al.*, 2011). Lacks of proper water supply to the root, high transpiration rates are the main reason of drought stress and it effects growth, development and ultimately the yield (Pandey and Shukla, 2015). Being a water loving crop, rice production gets severely impaired by drought stress; a 15% to 50% yield loss has been noted

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How to cite this article: Panja, S., Gupta, A.D. and Dey, N. (2024). Impact of Drought Stress on Grains Filling in Rice and its Management: A Review. Agricultural Reviews. 45(2): 282-289. doi: 10.18805/ag.R-2369.

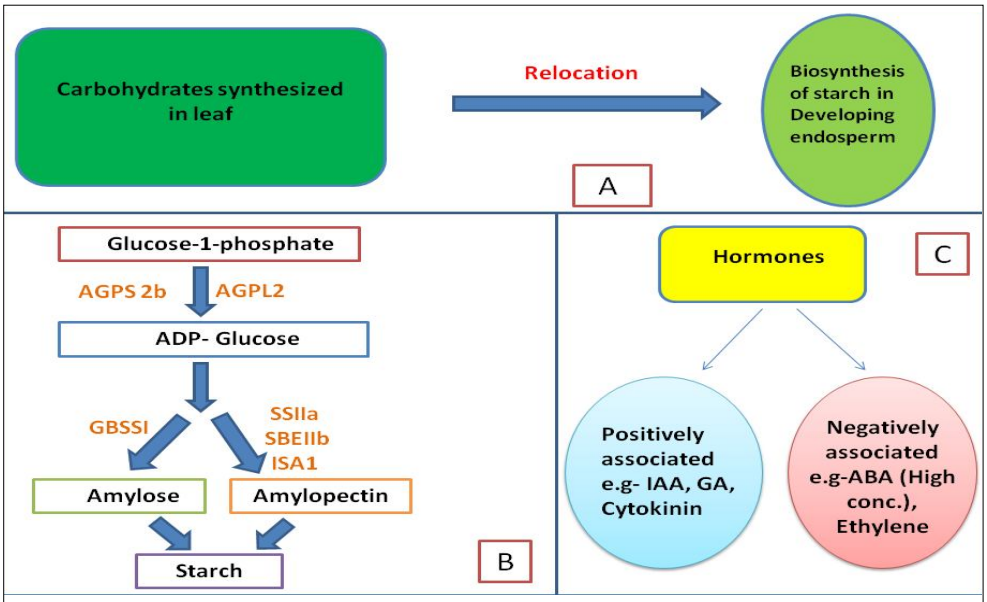
Submitted: 06-09-2021 **Accepted:** 14-01-2022 **Online:** 08-03-2022

depending on the vigour and period of stress given (Srividhya *et al.,* 2011). At the time of reproductive growth, a sharp decline in grain yield occurred when rice plant subjected to even moderate levels of drought stress (Venuprasad *et al.,* 2008). The yield of a grain crop is a function of the rate and duration of accumulation of dry weight in the economically valuable parts of the plant (Rahman and Yoshida, 1985). Besides grain size, the duration and rate of grain filling also determine the final grain weight and thereby contribute greatly to grain productivity (Takai *et al.,* 2005). In two recent reports (Berahim *et al.*, 2021; Kumar *et al*., 2021) the effect of induced drought was studied on different yield related parameters along with stomatal performances. Four components contribute to potential rice grain yield that are grain weight, grain number per panicle, panicle number per plant andthe ratio of filled grains (Sakamoto and Matsuoka, 2008). It has been documented that grain weight was largely determined by grain filling (Wang *et al*., 2008). Rice grain filling is nothing but a process of starch accumulation, as starch contributes 80% to 90% of the final dry weight of brown rice (Zhu *et al*., 2011). Grain filling is a process which occurs as a complex series of events, including the relocation of carbohydrates synthesized by photosynthetic organs and biosynthesis of starch from sucrose in the developing endosperm (Peng *et al*., 2013). The main component of rice endosperm is starch and thus incomplete grain filling is generally due to defects in starch synthesis (Zhu *et al.,* 2011). In hybrid cultivars, the vital reason for fluctuation in grain yield is attributed to poor grain filling of the later-flowering spikelets of rice, which is itself is a serious problem (Yang and Zhang, 2010). As a result of climate change, there is a possibility of reduction of yield, in a limited water resource (Ray *et al*., 2015). In two independent studies (Melandri *et al*., 2021 and Panda *et al*., 2021) reported all the different mechanisms behind the drought tolerance in rice in details. A recent report made by Kumar *et al.* (2020) showed that drought have a major role in quantity and chemistry of resistant starch content and Glycemic index of rice grain during development. Therefore, research on the grain filling in rice in response to stress is essential for us to increase our understanding to employ strategies to combat drought stress, through which grain weight can be enhanced, consequently increasing the grain yield per plant (Peng *et al.,* 2013). For that reason, basic requirement is to know the mechanism of drought tolerance potentiality of plant for better yield in limited rainfall (Mostajeran and Rahimi, 2009). It can be achieved through development of short duration high yielding lines through breeding or transgenics, which may give better yield under environmental stress (Singh *et al*., 2012). Considering this significant requirement and lacunae, an initiation was taken in present study where a detailed account has been taken on biochemical basis and mechanism of grain filling during developmental stages and how drought alter the grain filling mechanism. Finally, the possible management practices which can be employed to overcome the effect of drought on grain development stage have been discussed.

Grain filling in rice

In rice, the flowering stage is vital, as it is the stage when the meiosis cell division starts andafter that panicle initiation starts from flag leaf (Biswal and Kholi, 2013). Grain filling is mainly visible when a milky liquid fills the grains, this is the main reason for the increase of dry weight of the grain (Zhang *et al.,* 2012). Rice grain filling is a process of starch accumulation since starch contributes 80% to 90% of the final dry weight of an unpolished grain (Duan and Sun, 2005). Initially from sucrose, biosynthesis of starch takes place in the developing endosperm which in turn determines grain yield and rice quality (Zhu *et al.,* 2011). Roles of several crucial enzymes have been documented in the pathway of starch synthesis and (Tetlow *et al.,* 2004); these are sucrose synthase (*SUS*), UDP-glucose pyrophosphorylase (*UG Pase*), ADP-glucose pyrophosphorylase (*AGPase*) andstarch synthase. Among these *Sus3* is highly specific to the grain (Huang *et al*., 1996). Starch synthase has been found to exist in two different forms and these are granule-bound starch synthase (*GBSS*) and soluble starch synthase (*SSS*) (Zhu *et al.,* 2011). *GBSSI* is also called Waxy (*Wx*), both *Wx* and *SSIIa* are highly specific for grains (Chen *et al*., 2012). Synthesis of amylopectin is more complicated than amylose and involves all four types of enzymes including AGPase, *SSS*, Starch branching enzyme (*SBE*) andstarch de branching enzyme (*DBE*) (Jeon *et al.,* 2010). It was observed that after 3 days to 15 days from pollination, some phytohormones like Auxin, ABA and Zeatin concentrations notably increased (Abu *et al.,* 2012). Cytokinin levels in rice spikelets are significantly correlated with seed development (Zhang *et al.,* 2009). Negative correlation has been found between levels of ethylene in developing seeds and enzymatic activities linked with starch metabolism eventually leading to poor grain filling, for instance more ethylene levels in developing seeds leads to poor grain filling (Zhang *et al.,* 2009). A detailed description of the metabolic pathways associated with sucrose to starch conversion in developing grain particularly during grain filling stage was recently reported by Jiang *et al.* (2021). Comparative genomics study through transcriptome profiling among two rice genotypes under mild drought during grain-filling stage was conducted by Liang *et al.* (2021) and in a suppressed transgenic line of the *OsSYT-5* gene, Shanmugam *et al.* (2021) reported the enhanced photosynthetic rate with reduced stomatal conductance and transpiration under water deficit condition. A diagrammatic flow chart describing the major biochemical pathways associated with grain filling in rice in described in Fig 1.

It was noted that when concentrations of ABA increased, transportation of sucrose into the grains got reduced which lowered the ability of grains to synthesize starch (Bhatia and Singh 2002), surprisingly it was also seen that optimum concentrations of Abscisic acid (ABA) augmented SUS activity (Tang *et al.,* 2009). During embryo development, it



A- Carbohydrates translocation from source to sink, B- Major grains specific enzyme unit involved in starch biosynthesis in developing endosperm, C- Major hormones associated with grains filling.

Fig 1: Different aspect of grain filling in rice.

was observed that enhanced Gibberellic acid (GA) concentrations at initial grain filling stages contributed significantly towards rapid enlargement of the embryo (Yang *et al.,* 2002).

Key changes during drought stress in rice

When drought occurs, usually plant growth rate reduced (Zhu *et al,* 2004) and poor root development happens with reduced leaf surface (Pandey and Shukla, 2015). Leaf rolling is a common phenomenon and it is used as a criterion for scoring drought tolerance (Kadioglu and Terzi, 2007). As turgor pressure reduces under stress, cell growth severely decreases (Taiz and Zeiger, 2006). Common effects of drought stress are mainly reduction of germination (Swain *et al*, 2014), inhibition of plant height as well as growth (Sokoto and Muhammod, 2014) and also reduction of panicle number (Bunnag and Pongthai, 2013). Net photosynthesis (Yang *et al,* 2014) and rate of transpiration are also affected by water stress (Cabuslay *et al,* 2002) along with stomatal conductance (Singh *et al.,* 2013). It has been proved that drought affects efficiency of water utilization and reduces photosynthetic rate of rice plants. (Yang *et al.,* 2014). Drought reduces photosynthesis in flag leaf by inhibiting PSII activity (Pieters and Souki, 2005). Rubisco enzyme activity sharply decreases during drought, which is the key enzyme of the Calvin cycle (Zhou *et al*., 2007). Decrease in chlorophyll content has also been reported on drought stressed rice plants (Maisura *et al*., 2014). A positive correlation is present between relative wWater content (RWC) and water use efficiency (WUE) during drought stress but transpiration rate has negative correlation with WUE (Akram *et al*., 2013). In cytoplasm, several osmolyte accumulates for osmotic adjustment, among these proline was found to play a major role in drought stress tolerance mechanism (Pandey and Shukla, 2015). It was observed that accumulation of soluble sugars was also induced during drought (Maisura *et al*., 2014). Proline acts as an osmolyte and it helps for better maintenance and also imparts drought tolerance (Vajrabhaya *et al*., 2001). Some positively charged molecules like Polyamines (PAs) are also involved in the response to drought (Calzadilla *et al*., 2014). Reactive oxygen species (ROS) generation is a common phenomenon in response to drought stress (Faize *et al*., 2011), which includes super oxide radical and others free radicals like hydrogen peroxide and several forms of singlet oxygen. In plants, ROS generation is the main reason for protein, nucleic acid damage and also lipid peroxidation (Pandey *et al*., 2015). Up-regulation of 5000 genes and down-regulation of more than 6000 genes were observed in rice during drought period as reported (Maruyama *et al*., 2014). Up regulation of *DREB* transcription factors in response to drought also play major role in ABA-independent pathway, particularly two transcription factors, *OsDREB2A* and *OsDREB2B* expression are in high levels during water stress (Matsukura *et al*., 2010). The *OREB1bZIP*-type transcription factor also regulates the ABA-dependent pathway in rice (Hong *et al*., 2011). A summary on overall impact of drought stress on rice plant is presented in Fig 2.

Impact of drought on grains filling

Three phases during rice plant development that have an impact on grain yield are: Vegetative, reproductive and ripening stages in which drought conditions cause spikelet sterility and unfilled grains (Ndjiondjop *et al*., 2010). It was

found that drought stress impaired seed germination and early seedling growth, reduced plant growth and development in the vegetative phase, delayed flowering at the reproductive phase anddecreased the rate of grain filling (Ndjiondjop *et al*., 2010). Due to water stress, photosynthesis in leaf and flag leaf gets reduced which affects grain filling and which results in low yield in rice (Pandey and Shukla, 2015). During drought stress, reduction of seeds setting was observed with grain size and weight, due to spikelet sterility (Raman *et al*., 2012). During booting stage, drought stress can effect in various ways (Pantuwan *et al*, 2002), like floret initiation is interrupted by flowering in terminal periods, resulting in slow grain filling and spikelet sterility, eventually causing low grain weight and as a consequence of which poor paddy yield (Pandey and Shukla, 2015). Reduction in grain yield due to drought occurs probably by decreased grain filling period (Shahryari *et al*., 2008) along with disruption of leaf and gas exchange properties and the most important grain filling, source and sink translocation also gets affected due to drought stress (Farooq *et al*., 2009). Water stress can decrease pollen viability by degrading starch of pollen, as result of which pollens grains fail to fertilize the egg (Liu *et al*., 2006). Sterile panicles increase due to drought in booting phase (Pantuwan *et al*., 2002) and mild drought in grain filling stage can decrease yield upto 14.7% (Cai *et al*., 2006), whereas upto 52% yield loss was observed due to severe drought during grain filling (Yambao and Ingraml, 1988). In drought stressed tice plants, it was observed that ethylene concentration increases in the rice grain at the early grain-filling stage but decreases during grain development (Yang *et al*., 2004). Significant yield devastation occurred when water stress was perceived during flowering stage (Yang *et al*., 2004). Since drought can directly affect flowering, it also results in abortion of flower and one of the major causes for unfilled grain formation and grain abscission (Hsiao *et al*., 1976). High percentages of unfilled grains were also noted due to drought during reproductive growth stage (Davatgar *et al*, 2009). This happens because of reduction of assimilate translocation towards tiller of the plant (Rahman *et al*., 2002). Key enzymes which played an important role in active grain filling process includes enzymes like invertases, sucrose synthase, ADP glucose pyrophosphorylase (AGPase) andstarch synthase as well as the starch branching and the debranching enzymes all of which are affected by drought stress (Sheoran and Saini, 1996). Delayed in flowering time due to water stress was found to be closely associated with filling of grains that ultimately hampered the crop yielding (Pantuwan *et al*., 2002).

Management of drought stress for better grains filling and yield

Management through transgenic rice

One of the modern management strategies for drought stress is the development of transgenic rice. In such transgenic rice, over expression of *OsDREB2A* and *OsDREB2B* genes have been found to increase drought tolerance (Cui *et al*., 2011). ROS accumulation and its subsequent modulation by manganese superoxide dismutase, an anti-oxidant enzyme encoded by transgenic rice plants over expressing the gene *mnSOD* have resulted in superior osmotic tolerance (Wang *et al*., 2005). Several traits of rice which include spikelet fertility, grain filling and major yield traits like panicle number per plant, grain number per plant can be achieved through cultivation of transgenic rice plants over expressing *NAC5* (Jeong *et al*., 2013). Drought tolerant transgenic rice plants over expressing *OsOAT* have also increased heading than normal rice, in response to drought during panicle heading stage (You *et al*., 2012). In transgenic rice, it was seen that grain yield was

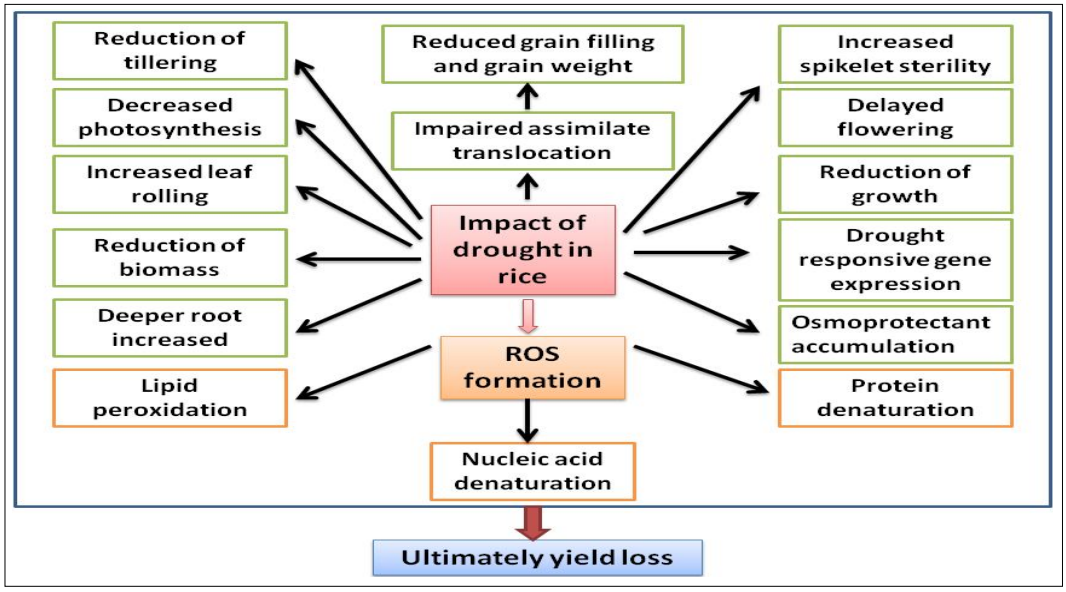


Fig 2: Overall impact of drought stress on rice plant.

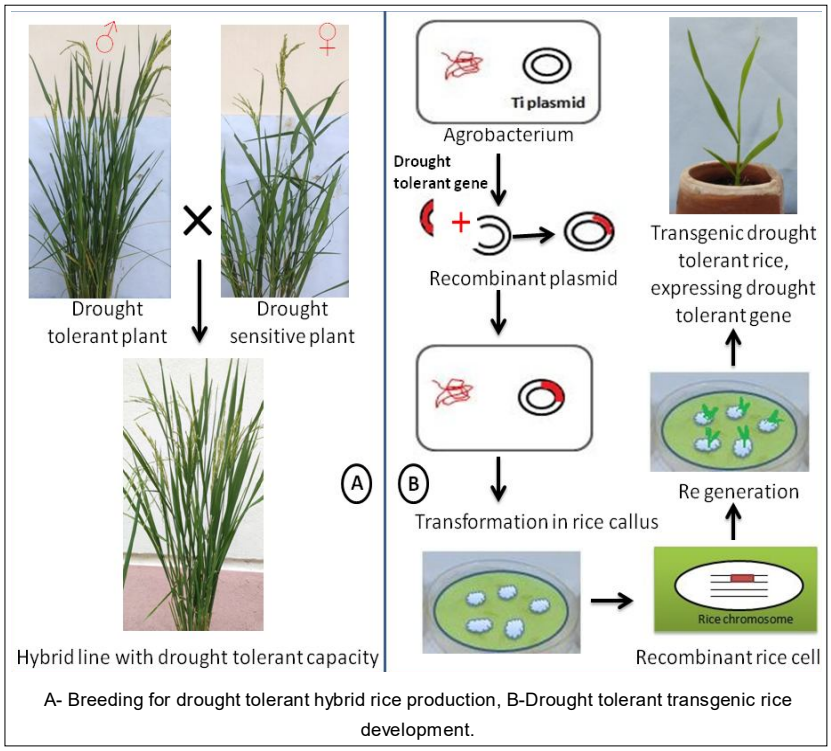


Fig 3: General approach of drought stress management.

high through high grain filling during drought condition in field on the time of heading and this was observed as a result of over expression of *AP37* gene along with other transcription factor, *AP2/ERF* (Oh *et al*., 2009). Improvement of drought tolerance by silencing OsSYT-*5* gene has been reported by Shanmugam *et al*. (2021).

Management through hybridization

The first step towards development of drought tolerant crop plants is the identification of genetic variation responsible for drought resistance (DR) but improvement of such desirable DR attributes in crop plants is a critical challenge for plant breeders and crop physiologists since the drought resistance involves a complex genetic trait with multiple pathways (Basu *et al*., 2016). Drought management is possible through development of short cycle hybrid rice, with very fast reproductive cycle and which are able to produce seeds before on set of drought stress (Yue *et al*., 2006). Farming of such short duration cultivars is effective as it has short grain filling period and these rice lines possessing various adaptive mechanisms which helps to escape terminal drought occurring during the reproductive stage. Hybrid rice with long flag leaf has great positive impact on yield under drought stress (Kumar *et al*., 2021). Hybrid varieties can tolerate drought by controlling stomatal opening and water conduction in root by producing Spermidine (SPD) (Berahim *et al*, 2021).

An overview on general approach of drought stress management in rice is presented in Fig 3.

Conclusion and Future Research Perspective

Development of drought tolerance in crop plants such as rice is tricky and challenging task that involves comprehensive in-depth understanding of the various characters that govern grain filling for better yield, under drought conditions. These characters range from morphological to physiological as well as include characters that range from molecular to biochemical. It has been widely observed that variations of different components in wild species of rice lines which grow in drought prone regions contain genotypes that have evolved and are well adapted as a result of natural selection. These wild species having drought tolerant properties can be introgress in to sensitive line for increased yield potentiality. Also, more investigations are required to understand the interplay of endogenous phytohormones and its optimum concentrations that imparts drought resistance and improves grain filling in rice. Usage of advanced phenotyping platforms for selection of genotypes responsible for drought resistance will help in the identification of Quantitative Trait Loci (QTL) and genomic regions that contribute to drought resistance. There may be a good number of related traits, which govern the grain development collectively under drought stress, identification of which are necessary to understand and establish, which of the traits are primary contributors to grain yield in rice plants. Nevertheless, the practical and promising way of selecting potential rice genotypes through breeding

programmes is to observe grain yield under drought, a yardstick which will eventually lead to the development of high yielding drought resistant cultivars. In addition to molecular breeding approaches, genetic engineering of regulatory genes, which are responsible for grain filling and high yield will also be essential in future for our food security during water scarcity.

ACKNOWLEDGEMENT

Authors are grateful to DRDO/LSRB, Government of India, for financial support, in the form of a major research project of 2017 (Ref.No-LSRB303) and also UGC Non NET fellowship.

Conflict of interest

The authors declare that they have no conflicts of interest, including financial and non-financial competing interests.

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