



# DREB1C: Connecting Dots Between Water- and Nitrogen-Use Efficiency to Climate-Smart Crop Development

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Received: 22 December 2022 / Accepted: 17 October 2023

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## Abstract

Complex traits like water use efficiency (WUE) and nitrogen use efficiency (NUE) are directly associated with crop yield and their stress-tolerant capacity. For developing climate-smart crops, it is crucial to identify new targets for capitalizing the benefits of WUE and NUE. However, understanding the molecular mechanism of WUE and NUE and their coordination with stress mitigation/signalling pathways are complicated. A multi-stress responsive transcription factor, *Dehydration-Responsive Element Binding Protein 1C* (*DREB1C*) has recently been recognized as a key component of nitrogen use efficiency (NUE) and yield in rice. Our data mining bioinformatic analysis suggest that *DREB1C* may be involved in signaling pathways of different hormones such as abscisic acid (ABA), ethylene, gibberellin (GA), and methyl jasmonate (MeJA). Our investigation also indicates that *DREB1C* is involved in various stress mitigation and signaling pathways, including drought, salt, cold, anaerobic environments, phosphorous starvation, and response to the rice blast fungus. Furthermore, repository data suggests that *DREB1C* may also be involved in morpho-physiological processes by controlling genes such as small subunits of ribulose-bisphosphate carboxylase, chlorophyll A/B binding protein, and protochlorophyllide reductase. Taken together, we emphasize the role of *DREB1C* in responding to climate-driven episodes of combined stress, with particular emphasis on to two broad-spectrum traits: WUE and NUE. In this short synthetic review, we make an effort to highlight the underlying connections of *DREB1C* with plants' responses to drought and limited nitrogen conditions and emphasize its potential for future climate-smart breeding programs.

**Keywords** DREB1C · Water-use efficiency · Nitrogen-use efficiency · Stress tolerance · Yield · Rice

## Abbreviations

DREB Dehydration-Responsive Element Binding Protein  
NUE Nitrogen-use efficiency  
WUE Water-use efficiency  
N Nitrogen  
C Carbon

AP2 APETALA2  
ERF Ethylene Response Factor

## Introduction: Effect of Climate Change on WUE and NUE

Water and nitrogen (N) are two absolutely essential components of plant life systems and play crucial roles in the growth and development. Optimum soil moisture, along with the coordination of N uptake and transport, is essential for plant survival. Water use efficiency (WUE) and nitrogen use efficiency (NUE) in plants are highly relevant to climate resilience, yet their molecular mechanisms remain to be fully understood (Rivero et al., 2022; Mondal et al. 2023).

Global warming and climate change are impacting the frequency, dynamics, and intensity of various abiotic and biotic stresses, including drought, temperature fluctuations, salinity, and pathogens, leading to yield losses worldwide (Rivero et al., 2022). Agriculture is the largest consumer

Handling Editor: Vinay Kumar.

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of water globally, accounting for 70% of freshwater usage (Connor et al., 2017). Gupta et al. (2020) reported that drought-related crop yield losses amounted to \$30 billion over the last decade, and climate change is expected to reduce freshwater availability by approximately 50% by 2050.

WUE plays a crucial role in determining crop performance under water-limited conditions and breeding for high WUE will facilitate sustainable water use in agriculture. On the other hand, in many agricultural regions worldwide, N is considered the most limiting factor for cultivation (Fageria and Baligar, 2005). The excessive application of N fertilizers and subsequent reductions of N uptake efficiency also affect flowering times and crop yields (Anas et al., 2020). In the current climatic context, developing breeding strategies to produce crops with high NUE has become a prime focus, as a mere 1% increase in NUE could annually save \$1.1 billion (Kant et al., 2011). Therefore, identifying the molecular basis of WUE and NUE is crucial for pinpointing candidate genes for climate-smart breeding programs.

### Dehydration-Responsive Element Binding 1 (DREB1), a Unique Family of Transcription Factor in Angiosperm

Transcription factors (TFs) are considered as determining factors of the first level of gene regulation. The APETALA2/Ethylene Response Factor (AP2/ERF) superfamily is one of the largest TF families, and its members are involved in the regulation of growth and development, as well as in responses to a range of biotic and abiotic stress responses in plants (Li et al., 2020). Based on the amino acid sequence of their DNA binding domain, the ERF family can be further divided into two subfamilies: Group A, which includes *Dehydration-Responsive Element Binding Protein (DREB1)/C-repeat-binding factor (CBF)*, and Group B, which constitutes the *ERF* subfamily. Phylogenetic analysis indicates that *DREB1/CBF* family genes predominantly evolved in Angiosperms, and the monocot-specific abundance of clades I and II may have specific functions in monocots (Li et al., 2020). DREB1 proteins bind to the CRT/DRE sequence (G/ACCGAC) within the promoters of downstream stress-inducible genes, conferring tolerance to multiple stresses in different crops (Sarker et al., 2019).

### DREB1 is AVital Family of TF for Multi-Stress Adaptation

To understand plant adaptation, the identification and characterization of transcription factors (TFs) have been considered as one of the most suitable approaches for decades, as TFs modulate metabolic processes, growth, development, and stress adaptation by regulating target genes. Song et al.

(2021) identified a total of 146 *Arabidopsis* genes that are distinct targets of CBF/DREB1, and these targeted genes are involved in abiotic stress responses, hormones, and environmental signaling. Overexpression of *AtDREB1A*, *AtDREB1B*, and *AtDREB1C* conferred improved tolerance to freezing, salt, and drought in *Arabidopsis* (Liu et al. 1998; Kasuga et al. 1999; Gilmour et al. 2004; Zhang et al. 2023). Similarly, *AtDREB1F* overexpression in *Arabidopsis* enhanced tolerance to freezing, drought, and heat (Kang et al. 2011), while overexpression of *AtDREB1D* enhanced drought tolerance in soybean (Guttikonda et al. 2014). Experimental evidence also indicates that the *OsDREB1* play a decisive role in response to cold, high salt, and/or drought conditions in rice (Dubouzet et al. 2003a, b). Transgenic rice overexpressing *AtDREB1A* exhibited significantly increased tolerance to dehydration, whereas overexpression of *OsDREB1B* was found to be more efficient for salt tolerance (Datta et al. 2012). Overexpression of *DREB1* genes from cotton, soybean, and zoysia grass have been shown to enhance tolerance to chilling, drought, heat, and salt (Gao et al. 2005; Shan et al. 2007; Kidokoro et al. 2015). A recent study showed that *OsDREB1C/E/G* genes are involved in heat, drought, and salt stress tolerance in rice (Wang et al. 2022). Novillo et al. (2004) demonstrated that the ability of *DREB1C* to negatively control the expression of *DREB1B* and *DREB1A* is crucial for stress endurance in *Arabidopsis*. Hence, functional analysis implies there is a coherent link between DREB1 and multi-stress adaptation in both monocot and dicot systems. These findings expand our knowledge of the roles of DREB1 proteins in plants, enhance our mechanistic understanding of abiotic stress tolerance, and will facilitate the generation of stress-tolerant crop plants.

### DREB1C-Mediated Drought/Dehydration Adaptation Through Enhancing WUE and Osmotic Adjustment

An advanced understanding of the relationship between crop yield, drought tolerance, and WUE is a prerequisite for designing climate-smart crop varieties, specifically for adaptability in drought in combination with other abiotic stress. Stomata represent a critical target for enhancing WUE since they are crucial in controlling plant water use and carbon gain. Recently, there has been a lot of interest in understanding stomatal kinetics, although a little mechanistic insight has been gained. Stomatal kinetics may differ depending on the abiotic stress conditions (Rizhsky et al. 2004). For example, under water-limited conditions, the closure of stomata prevents excess water loss; however, stomata remain open to cool leaves via transpiration in response to heat stress. Moreover, recent literature suggests that stomata closure during combined stress conditions is directly or indirectly linked to a decrease in WUE (Rivero et al., 2022). Although *AtDREB1a*-expressing rice lines exhibited

enhanced stomatal closure upon drought stress (Datta et al. 2012), the direct linkage between DREB1C and stomatal kinetics has not been illustrated so far. Therefore, unravelling how and to what extent *DREB1C* is associated with drought/dehydration adaptation could assist in developing strategies for sustainable crop production under changing climate conditions.

In rice, a total of ten *DREB1* genes were identified to be involved in the signaling events of a range of abiotic stresses (Wang et al. 2022). Previous reports showed that *DREB1* is involved in drought tolerance in rice using over-expression lines (Ito et al. 2006; Datta et al. 2012; Huang et al. 2018; Muthurajan et al. 2021). Recently, Wang et al. (2022) suggested that loss-of-function (LOF) of *OsDREB1C* are more susceptible to chilling compared to the wild type (WT), and the gene is also involved in scavenging reactive oxygen species (ROS) as well as regulating cell death. The *OsDREB1C* gene positively regulates heat, drought and salt tolerance (Wang et al. 2022). Furthermore, many researchers have suggested that *DREB1C* is a promising target for cold and dehydration tolerance in various plants (Liu et al. 1998; Dubouzet et al. 2003a, b; Nakashima et al., 2006; Zeng et al. 2022). The promoter of *AtDREB1C* (CFB2) bind with calmodulin binding transcription activator (CAMTA3), indicating a calcium-signal-driven gene expression (Doherty et al. 2009; Pandey et al. 2013); however, further research is required for a deeper understanding and establishment of the molecular mechanism.

Liu et al. (1998) reported that genes involved in cold/dehydration tolerance can also be potential targets of drought tolerance, since, under both stress conditions, induction of abscisic acid (ABA) biosynthesis is common and shares similar types of mechanisms. Cellular dehydration is a common effect of stresses such as cold and drought; which in turn, activates common signaling pathways and changes metabolic profile (Guo et al., 2021). The production of osmoprotectants like raffinose, trehalose, fructose, proline, and glycine betaine under drought or cold stress to stabilize proteins, as well as cellular structures, is well understood in a wide range of plant species (Krasensky and Jonak 2012; Guo et al., 2021). *AtDREB1C*-overexpressed rice lines exhibited improved growth under moderate drought/osmotic stress through dehydration tolerance as well as by avoiding dehydration, notably by reducing water demand together with a reduction in growth time, which may be a consequence of osmotic adjustment (Ishizaki et al. 2013). Moreover, the study showed that improved survival, along with higher growth and yield under drought, was due to reduced water use. Despite inadequate molecular information, insights gained here suggest a strong correlation between *DREB1C* expression, osmotic adjustment, drought tolerance, and enhanced WUE, which provides a platform

for enriching further understanding of WUE and climate-smart crop production.

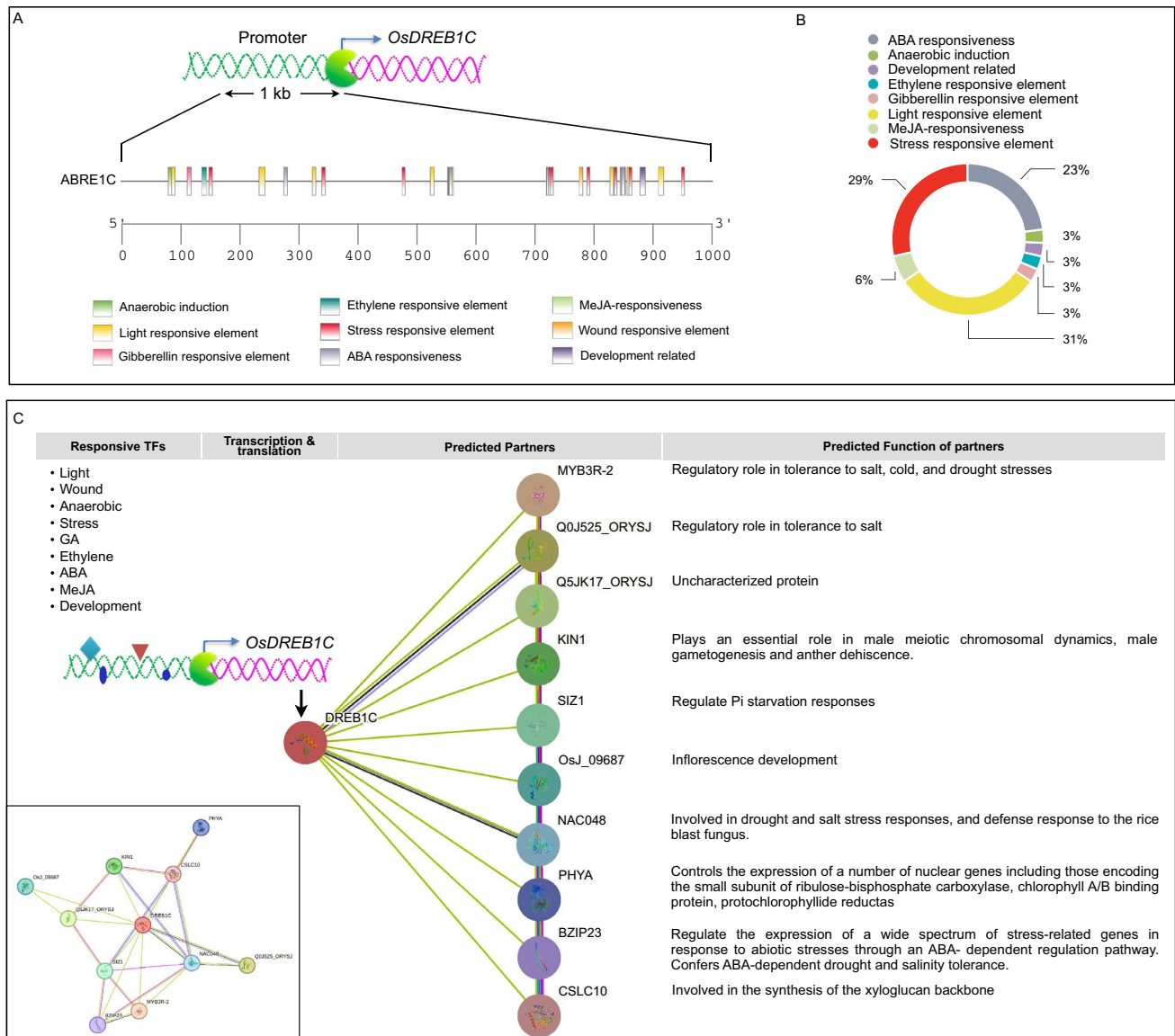
### ***DREB1C* is a Novel Target to Enhance NUE and Yield**

The amount of grains produced per unit of readily available soil N is the numerator of nitrogen use efficiency (NUE). Excessive nitrogen is applied in modern agriculture, which often delays flowering and ripening in major crops, including rice (Ye et al.; 2019; Zhang et al. 2021). Excessive N fertilizer use also leads to water contamination, reduced soil fertility, deteriorated soil health, and increased greenhouse gas emissions. Despite decades of research, the genetic architecture of NUE remains poorly understood because of an inadequate understanding of the coordination of nuclear and organelle protein expression, complex compartmentalized metabolic networks, and the intricacies of eukaryotic multilevel gene regulation (Mondal et al. 2021).

A recent study by Wei et al. (2022) identified significant expression of the DREB family of transcription factors under low-nitrogen conditions in rice based on RNAseq analysis. Many crucial genes, such as the nitrate transporters (*NRT1.1B*, *NRT2.4*), nitrate reductase (*NR2*), the flowering regulator (*FTL3*), and RuBisCO (*RBCS3*), are regulated by *DREB1C* through binding to their promoter regions. Overexpression of *DREB1C* in rice resulted in early seedling vigour, higher levels of photosynthetic pigments, increased RuBisCO content, elevated rates of photosynthesis, enhanced N uptake, and improved NUE. The *DREB1C*-overexpressing plants displayed a higher harvest index, increased remobilization of N and C to sink organs, and a significant reduction in flowering time and crop duration. Interestingly, field trials results revealed that the rice lines overexpressing *DREB1C* showed increased yield of about 41–68%, early maturity, and improved NUE (Wei et al. 2022). Further, *OsDREB1C* overexpression increased 17–22% yield in wheat and enhanced 14–35% biomass in *Arabidopsis* (Wei et al. 2022).

Our analysis of data from repository databases like PlantCARE (Lescot et al. 2002) and STRING (Franceschini et al. 2012) suggests the possible regulation and dynamic function of *DREB1C* in rice (Fig. 1). Promoter structure analysis suggests that *DREB1C* might influence responses to light, wounds, anaerobic conditions, and various stress conditions (Fig. 1A). Identified *cis*-regulatory elements (CREs) also indicate that *DREB1C*'s regulation is influenced by a range of plant hormones, including gibberellin (GA), ethylene, abscisic acid (ABA), and methyl jasmonate (MeJA) (Fig. 1B).

Furthermore, information generated from the STRING database implies that *DREB1C* is likely involved in different cellular and physiological functions through interactions with a range of proteins, including MYB3R-2, QQJ525\_ORYSJ

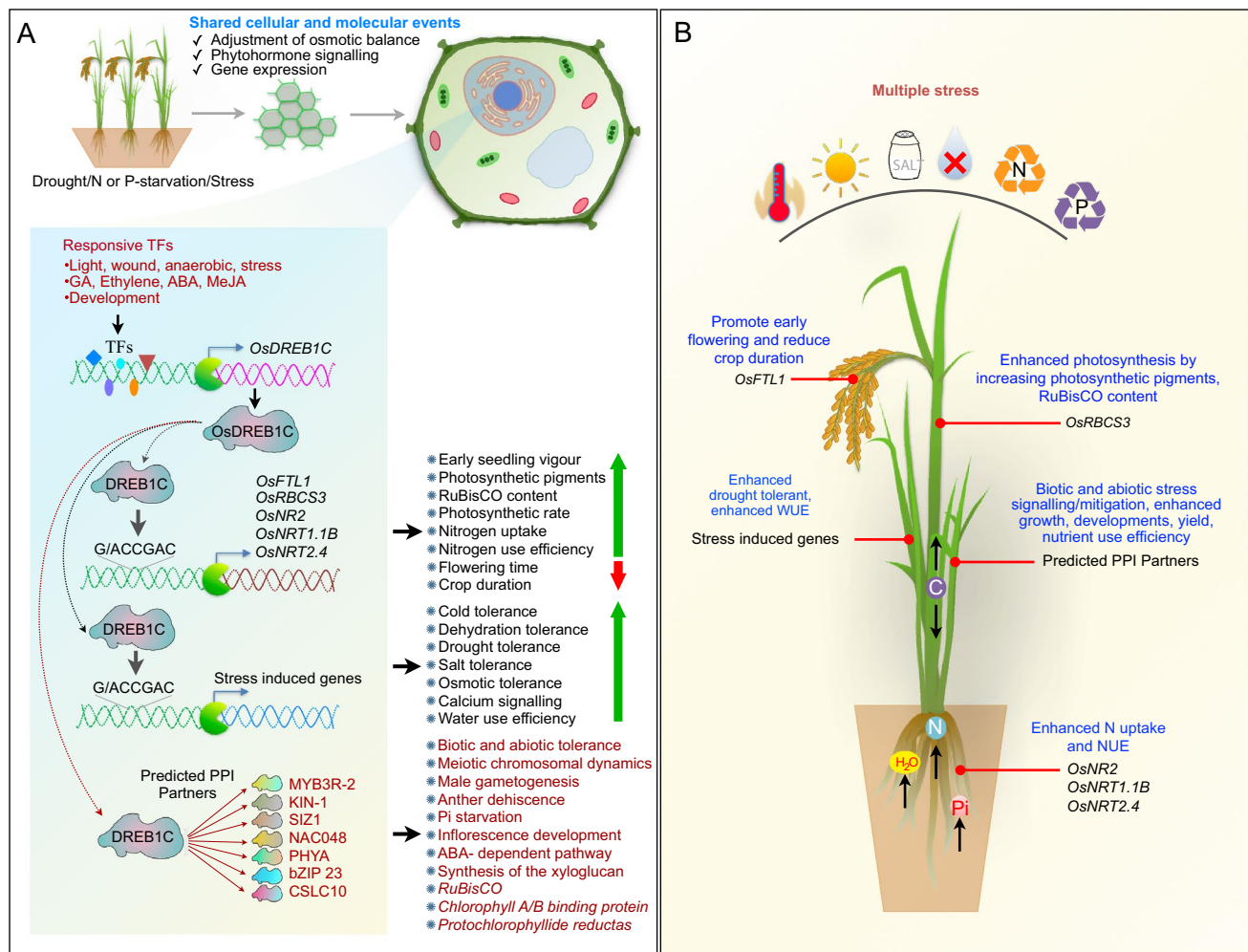


**Fig. 1** In silico promoter structure analysis, identification of *cis*-regulatory elements, and prediction of protein–protein interaction to understand molecular regulation and probable function of *DREB1C* in Rice. **A** Promoter structure analysis and distribution of *cis*-regulatory elements (CRE) across the length (1 kb) of the promoter of *OsDREB1C*. **B** Percentage (%) of distribution of identified *cis*-regulatory elements (CREs) such as ABA responsiveness, anaerobic induc-

tion, development-related, ethylene-responsive element, gibberellin responsive element, light responsive element, MeJA-responsiveness, stress-responsive element. **C** Predicted model representing the factors (light, wound, anaerobic, stress, and hormones) that modulate the expression of *DREB1C* and probable role in different molecular and physiological processes through interacting with other proteins. *ABA* abscisic acid, *GA* gibberelline, *MeJA* methyl jasmonate

(Os08g0474000), Q5JK17\_ORYSJ (Os03g0184500), kinesin-like protein KIN-1, SIZ1, NAC048, PHYA, bZIP 23, and CSLC10 (Fig. 1C). Functional annotation revealed that *DREB1C* is involved in abiotic stress responses (drought, salt, cold), biotic stress responses (rice blast fungus), and phosphorus starvation (Fig. 1C). *DREB1C*-interacting protein partners play essential roles in various cellular processes (e.g., male meiotic chromosomal dynamics, male gametogenesis, and anther dehiscence) and morpho-physiological

responses by regulating genes such as the small subunit of ribulose-bisphosphate carboxylase, chlorophyll A/B binding protein, and protochlorophyllide reductase. *DREB1C* may also regulate the expression of a wide spectrum of stress-related genes in response to drought and salinity stresses through an ABA-dependent regulatory pathway mediated by *DREB1C*-bZIP interaction.



**Fig. 2** Dynamic role of DREB1C in NUE and WUE in Rice. **A** Under drought and low-N conditions OsDREB1C directly binds to the promoter and up-regulates the transcripts of *OsRBCS3*, *OsNRT1.1B*, *OsNRT2.4*, *OsNR2*, *OsFTL1*, and different stress-responsive genes including drought, cold/dehydration, salt, and osmotic. In turn, enhanced the rates of photosynthesis, NUE, and WUE by reducing the flowering time as well as crop duration in rice. **B** *OsDREB1C* is an integrator of potential below- and above-ground traits like NUE, WUE, photosynthesis, and early flowering in response to climate

change-induced stress conditions such as high temperatures, light, limited water, and N conditions. Hence, *DREB1C* is poised to be a climate-smart TF. *DREB1C* Dehydration-Responsive Element Binding Protein 1C, *FTL3* flowering locus T (FT)-Like homolog, *NR2* nitrate reductase, *NRT1.1B/NTR2* nitrate transporters, *NUE* nitrogen-use efficiency, *Os Oryza sativa*, *RBCS3* Ribulose-1,5-bisphosphate carboxylase/oxygenase, *TF* transcription factor, *WUE* water use efficiency, *N* soil nitrogen, *H<sub>2</sub>O* soil water, *C* photosynthetic carbon

## Conclusion

Due to climate change, multiple stressors, including drought, heatwaves, nutrient scarcity, flooding, and salinity, may concurrently or sequentially affect various regions of the world. The adverse consequences of climate change are already evident, leading to detrimental effects on various pathways related to plant responses and stress adaptation, all orchestrated by distinct transcription factors (TFs). Recent investigation revealed the involvement of *DREB1C* in seedling vigour, elevating photosynthetic pigments accumulation, increasing RuBisCO content, and enhancing photosynthesis, increasing N uptake and NUE, as well as in multiple stress

tolerance. Our bioinformatic analysis suggests that *DREB1C* has immense potential as a candidate gene and is involved in a range of stress mitigation/signaling pathways. Modification of Cis-elements in the promoter of *OsDREB1C* with various genome editing tools could unravel many novel functions (Karmakar et al. 2022).

Collectively, we have emphasized the role of *DREB1C* in responding to climate-induced combinations of stresses, with particular emphasis on two versatile traits, Water Use Efficiency (WUE) and Nitrogen Use Efficiency (NUE), as key attributes for developing climate-resilient crops. It is intriguing to note that a single transcription factor can enhance yield to a great extent and significantly influence

both NUE and WUE in rice, as illustrated in Fig. 2. Furthermore, our discussion implies that *OsDREB1C* stands as a promising candidate for a climate-smart transcription factor, worthy of consideration in climate-smart breeding initiatives.

**Acknowledgements** The authors are grateful to the Directors of their respective institutes for the facilities. KM acknowledges the funding from Ignite Life Science Foundation, Bangalore, and National Agricultural Science Fund (NASF), New Delhi.

**Authors Contribution** RM and KM conceived the idea. RM and KM wrote the manuscript. RM prepared the figure.

## Declarations

**Conflict of interest** The authors declare that there are no conflicts of interest.

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