

Prospects for rice in 2050

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Abstract

A key to achieve the goals put forward in the UN's 2030 Agenda for Sustainable Development, it will need transformative change to our agrifood systems. We must mount to the global challenge to achieve food security in a sustainable manner in the context of climate change, population growth, urbanization, and depletion of natural resources. Rice is one of the major staple cereal crops that has contributed, is contributing, and will still contribute to the global food security. To date, rice yield has held pace with increasing demands, due to advances in both fundamental and biological studies, as well as genomic and molecular breeding practices. However, future rice production depends largely on the planting of resilient cultivars that can acclimate and adapt to changing environmental conditions. This Special Issue highlight with reviews and original research articles the exciting and growing field of rice-environment interactions that could benefit future rice breeding. We also outline open questions and propose future directions of 2050 rice research, calling for more attentions to develop environment-resilient rice especially hybrid rice, upland rice and perennial rice.

KEYWORDS

abiotic stress, biotic stress, heterosis, perennial rice, upland rice

1 | INTRODUCTION

The global population is expected to reach 9.7 billion by 2050 and peak around 10.4 billion in the 2080s (UN, 2022). This generates the enormous challenge to feed the world while staying within planetary boundaries (Rockström et al., 2020). This will not be trivial since climate change is severely exacerbating the frequency, the severity, and the unpredictability of various

environmental stresses, including heatwaves, cool weather and chills, droughts, floods, soil degradation, and the spread of various diseases and pests (Figure 1), adversely affecting agricultural efforts in securing food production (FAO, 2022a). Therefore, besides hunting for new food sources and food production systems, transforming the current agrifood system to inclusive, effective, sustainable and resilient is of particular significance in food security.

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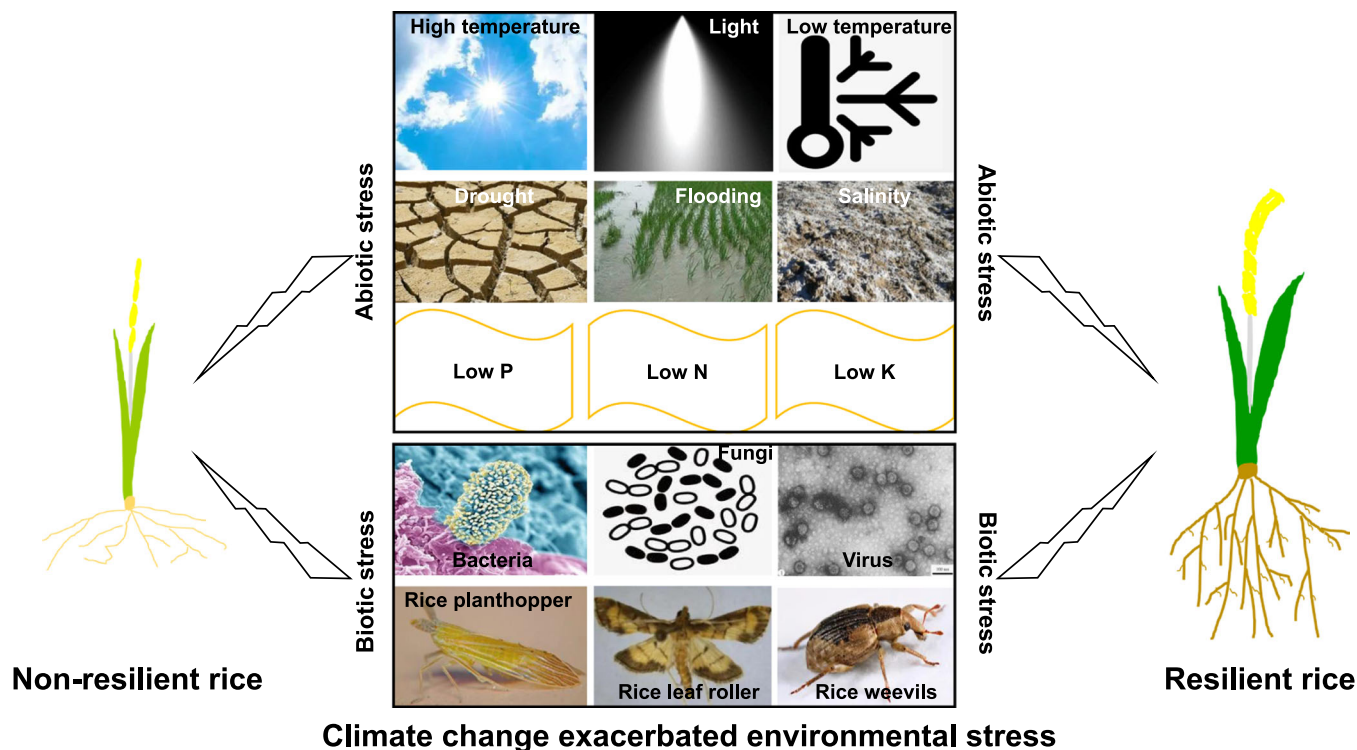


FIGURE 1 Types of abiotic and biotic stresses and their effects on ultimate growth performance of both nonresilient (current) and resilient (future) rice cultivars.

Rice is the main staple food that feeds more than half of the global population, and accounts for more than 75% of calory supply in some developing countries (Bin Rahman & Zhang, 2016). Although rice yield with a global production of 787.3 million tons in 2021 (FAO, <https://www.fao.org/faostat/en/>) has been improved by various agrotechnologies including genetic breeding, improving rice resilience to environmental stresses offers promise in ensuring sustainable rice production under changing climates (Dhankher & Foyer, 2018).

This Special Issue focused on recent advances in the fundamental understanding of rice-environment interactions and relevant progresses in resilient rice breeding, highlighting essential roles of future resilient rice in sustainable agriculture and food security.

2 | ABIOTIC RESILIENCE OF RICE

2.1 | Environment-sensitive genic male sterility (ESGMS)

ESGMS is a unique type of male sterility affected by both genetic and environmental factors. ESGMS lines form the core of the two-line hybrid rice breeding system because they can be transited into fertility as corresponding environment (photoperiod, temperature, humidity and others) changes, and play crucial roles in ensuring food security (Kim & Zhang, 2018). Cloning ESGMS genes and elucidating their underlying mechanisms are vital for the application of ESGMS line in rice hybrid breeding. Peng et al. (2022) summarized current

understanding of molecular mechanisms of ESGMS and their applications in rice hybrid breeding. The detailed molecular mechanisms of four types of ESGMS found in rice, namely PSGMS (photoperiod-sensitive GMS), TSGMS (thermal-sensitive GMS), HSGMS (humidity-sensitive GMS), and NSGMS (nitrogen-sensitive GMS), presented in this review (Peng et al., 2022), would benefit future efforts in overcoming bottlenecks that limit the application of ESGMS in rice two-line hybrid breeding.

2.2 | Heat and chilling stress

According to Intergovernmental Panel on Climate Change (IPCC), current global ambient temperature increased by 1.2°C as compared with preindustrial temperature (1850–1900), and this figure will likely approach 2.7°C by 2100 (IPCC, 2022). The rise of global ambient temperature seriously threatens the growth and yield of major crops, especially rice as it is extremely sensitive to high temperature from seedling stage to reproductive stage, and every 1°C increase in the global average temperature will lead to a 3.2% yield loss in rice (Muehe et al., 2019; W. Zhang et al., 2022). Currently, about 150 million hectares of rice worldwide are threatened by high temperature, and world's rice yield loss will be 40% in the next century due to negative effects of high temperature (Jagadish et al., 2015). The effects of heat stress on rice production, quality, physiology, heat-regulated genes and networks have been well summarized (Jagadish et al., 2015; Y. Yang, Yu, et al., 2022). Li et al. (2023), in this issue,

reviewed mainly recent advances in heat sensing and signalling, regulation of the heat stress response in rice, besides irreversible effects of heat stress on photosynthesis, reproduction, and quality in rice (J. Y. Li et al., 2023). The capacity of rice to balance heat stress response and growth, needs more attentions in future studies. It is well-known that brassinosteroids (BRs) play roles in the heat stress response in rice (J. Yang et al., 2021), but its underlying mechanism remains unknown. Zhang et al. (2022) reported that enhanced decomposition of BRs in young panicles is the cause of heat-stress-induced spikelet degeneration and yield loss. BRs can enhance heat resistance via suppressing spikelet degeneration by enhancing root activity, canopy traits and energy and antioxidant status in young panicles (W. Zhang et al., 2022), confirming that using BRs as chemical regulators could enhance rice resistance to heat stress (J. Yang et al., 2021).

On the other hand, cold and chilling stress is also a common global problem that causes yield loss in rice. It is reported that more than 15 million hectares of rice are threatened by cold weather globally, and rice cultivation is impossible in approximately 7 million hectares of land in south and Southeast Asia due to cold stress (Pradhan et al., 2019). Therefore, developing cold stress-tolerant rice varieties with high yield will help to grow rice in these vulnerable regions. Phenotypic, biochemical, physiological, molecular and cellular understanding of chilling tolerance in rice and novel approaches to speed up molecular design breeding for cold tolerance in rice varieties have been previously reviewed (Li, Zhang, Chong, et al., 2022). However, the ultimate solution to expand rice-planting to northern areas depends largely on the development of cold/chilling-tolerant cultivars, which needs mining and exploiting of key genes or alleles Zhang et al. reported in this issue that *bHLH57* can enhance trehalose synthesis, reactive oxygen species metabolism and CBFs/DREBs-dependent pathways, acting as a positive regulator of rice chilling tolerance, and that *bHLH57* can enhance seed setting rate and seed size, thus increasing grain yield (L. Zhang, Xiang, et al., 2023). Therefore, *bHLH57* is a potential target for future breeding for high-yielding, chilling-tolerant rice varieties.

2.3 | Salt stress

Salt stress, one of the important abiotic factors that affects cereal yield worldwide, takes up to 1.5 million hectares of farmland out of production annually and reduces productivity on approx. 46 million additional hectares (FAO, 2021, 2022b). Currently, more than one billion hectares and over 50% of the world's population are severely affected by salinity (T. Chen et al., 2021). The build-up of salt in the soil (top 30–100 cm) is the consequence of human-induced soil water processes, 62% irrigated land worldwide is affected by salinity (FAO, 2021). Among cereals, rice is the staple crop that is most sensitive to salinity stress. Although a recent review summarized advances in stress sensing and signalling, functional adaptation, and salinity tolerance breeding (T. Chen et al., 2021), understanding the complexity of salinity tolerance mechanisms in rice is still limited, and

real salt-tolerant rice varieties are not yet available. Wang et al. (2023) reported, in this issue, the new functions of a 14-3-3 protein, OsGF14b, in regulating stability and function of a previously known protein essential for rice salt tolerance, phospholipase C (OsPLC1), thus improving rice salt tolerance (N. Wang et al., 2023). Although effects of OsDG14b on grain yield and the potential of its incorporation into commercial germplasm were not investigated, this study will stimulate interests in 14-3-3 proteins.

2.4 | Low phosphate stress

Phosphate (P), a prominent nutritional constraint for rice production, is often limited in paddy field. Therefore, P-fertilizers are frequently overdosed to secure production. However, due to poor absorption efficiency, phosphate runoffs are causing eutrophication of aquatic and marine ecosystems and resulting blooms of toxic cyanobacteria, hence generating a serious environmental problem. Due to the non-recoverable depletion of global P resources, development of low P resilient rice cultivars is crucial for sustainable rice production, specifically cultivars with high P utilization efficiency. Despite the existence of many mechanisms explaining P scavenging and mobilization in rice plants (Dissanayaka et al., 2018; Watanabe et al., 2020), the genetic mechanisms remain largely unknown.

In this issue, Lu et al. (2022) reviewed the responses of root system, systemic Pi starvation signalling, internal P translocation and allocation, and *arbuscular mycorrhizal* symbiosis to orthophosphate (Pi) deficiency, as well as breeding practices to improve phosphorus use efficiency in rice (Lu et al., 2022). Lu et al. (2022) also proposed future directions for basic and applied studies on rice-low P interactions to facilitate the development of rice cultivars with enhanced phosphorus use efficiency through molecular design breeding (Lu et al., 2022). Guo et al. (2022) characterized roles of three SPX-MFS proteins in maintaining P homeostasis in rice vacuoles, the primary intracellular storage compartments for P in rice cells. Their findings indicate that alteration of vacuolar Pi sequestration could potentially enhance rice performance under low P condition (Guo et al., 2022), providing a new strategy to rational design P-efficient genotype that are less dependent on P-fertilizers.

2.5 | Light stress

Although rice is a short-day plant and usually grown in the wet season when solar radiation decreases to 40%–60% of its peak, long-term low light or dark caused by cloudy and rainy conditions often reduces rice production by up to 50%. Generally, low light adversely affects photosynthesis and induces premature leaf senescence, resulting in reduced yield and quality (Gad et al., 2021). Li et al. (2023) found that low light inhibits pollen tube elongation in rice and that the heterotrimeric G-protein α -subunit (RGA1) prevents the cessation of pollen tube growth induced by low light stress and enhance fertility through improving the metabolism and allocation of

sugars as an energy source in the pistil (H. Li, Feng, et al., 2023). Da et al. (2022) investigated the membrane-anchoring mechanism of leaf-form ferredoxin-NADP⁺ oxidoreductases (LFNRs) and their physiological roles in rice. They revealed that mutants of *OsLFNRs* and their putative anchor partners adversely affect electron transfer rate and growth, which is different from findings in *Arabidopsis*, and that *OsTIC62*, highly expressed in the dark, as compared to light, is necessary for LFNR-thylakoid membrane binding (Da et al., 2022). These two studies provided new targets for pollen tube growth and photosynthesis improvement in rice.

2.6 | Drought and flooding stress

Rice is usually grown in hot and wet areas, flooding and drought, two most prevalent climate disasters, often adversely affect rice growth and development, causing yield loss globally. Currently, over one-third of the global cultivated rice is affected by drought stress, 33% in developing countries, 25% in developed nations and 42% in under developed countries. It is predicted that globally over 15–20 million hectares of irrigated rice may suffer from some degree of drought by 2025 (Bouman et al., 2007), accounting for over 12% of total global harvested rice area in 2021 (FAO, <https://www.fao.org/faostat/en/>). Effects of drought on rice growth, development, production, and quality, as well as physiological and molecular responses have been reviewed previously (Panda et al., 2021; Y. Yang, Yu, et al., 2022). Sharma et al. (2022) deepened understanding of drought resistance in rice and further promoted efforts in developing drought-resilient rice varieties. They report that *OsFBX257*, a stress-induced F-Box protein, is indispensable for drought tolerance and maintenance of grain yield under drought conditions via positively modulating root depth and abscisic acid (ABA) responses in rice (Sharma et al., 2022). Sharma et al. (2022) propose that *OsFBX257* is a hub gene of a molecular network involving at least *OsCDPK1-GF14c* and *OsSAPK2-OsPP2C08* two signalling pathways (Sharma et al., 2022), which could be a potential target for breeding drought-resilient rice.

As compared with drought resistance, much more is known about molecular mechanisms of resistance and adaptation of rice to flooding, and flash flood-tolerant varieties have been successfully released to farmers in several Asian countries (Bin Rhman & Zhang, 2016). Seed anaerobic germination and seedling establishment are both critical for rice to survive at the early stages under flood conditions. Yin et al. (2022) summarized, in this issue, roles and molecular mechanisms of ethylene in the regulation of coleoptile elongation under anaerobic conditions, highlighting interactions of ethylene with other hormones, such as ABA, auxin, jasmonic acid (JA), and gibberellin (GA), in this process (Yin et al., 2022). This review should facilitate the manipulation of key genes for better performance under flood conditions in rice. Lee et al. (2022) reported that auxin is also necessary for rice to adapt to anaerobic germination and seedling establishment; they showed that reduced endogenous IAA enhances rice anaerobic germination tolerance and promotes seedling establishment in rice while excessive accumulation of IAA

leads to poor seed germination and seedling establishment, suggesting that there is a certain threshold value for auxin to function in anaerobic germination and seedling establishment (Lee et al., 2022).

2.7 | Floral transition

Floral transition, also known as heading date in rice, is a critical agronomic trait that determinates successful rice reproduction and ultimately yield. It has been selected for during rice domestication and improvement (Cao et al., 2021). Understanding the molecular events that underlie floral transition is of particular importance in developing resilient rice cultivars with shifted or fine-tuned floral transition traits that are more adaptive to changing environmental and developmental factors. Osnato (2022) summarized in this issue the genetic and evolutionary bases of flowering genes in rice, compared key flowering genes present in Asian (*Oryza glaberrima*) and African (*Oryza sativa*) rice cultivars, and presented progresses achieved in crossing between these two species aiming to combine stress tolerance of African rice with productivity of Asian rice (Osnato, 2022), one reasonable strategy to achieve environmental resilient rice cultivars to guarantee food security. Yoon et al. (2022) report the new finding that RICE FLOWERING LOCUS T 1 can promote floral transition in rice inflorescence meristem through direct binding to promoter regions of two auxin biosynthesis associated homeobox transcription factor encoding genes (*OsZHD1* and *OsZHD2*) and stimulating their expressions (Yoon et al., 2022), which provided molecular understandings of florigens in responses to both environmental and developmental clues.

2.8 | Rice responses in paddy field to real microclimate

Over the past decades, we have witnessed constant increase in the understanding of the plant response to various abiotic stress at anatomical, physiological, biochemical, molecular and genetic levels, which has brought the cloning and characterization of many stress-responsive genes. However, only few successful cases of transferring knowledge to breeding practice to solve problems in rice paddy field have been reported, likely because knowledge generated in controlled laboratory environments may not apply to the field situation. In the paddy field, rice plants experience not only a single stressful condition as in a typical laboratory setting, but rather a mixture of multiple stressors, such as light, temperature, water, and nutrient stresses, for its whole life rather than a specific growth stage as in the laboratory (Figure 1). Therefore, it is crucial to conduct studies in the field to obtain molecular knowledge that can reflect the physiological behaviour of rice in a real-world environment. Matsunami et al. (2022) report on a pioneering transcriptomic study, using both root and leaf samples taken from rice plants grown in the paddy field, from 29 days after transplanting (DAT) to 107 DAT, for a total of 41 days

intermittently. This study provides the first “in natura” study on the transcriptomic response of rice tissue to meteorological factors, and revealed stage-dependent transcriptomic responses of rice tissues to microclimate (Matsunami et al., 2022), providing important insights into rice physiology under changing climates.

3 | BIOTIC RESILIENCE OF RICE

During growth and development, different parts of rice plants are easily infected by many pathogens, including bacteria, fungi, virus, nematodes and insect pests, causing a global 30% yield loss per hotspot (Savary et al., 2019). To reduce biotic stress-caused yield loss in crops, the application of plant-protective chemicals is currently the most effective way, which might be associated with environmental tradeoffs. Although in recent decades more emphasis has been put on developing biologicals (Collinge et al., 2022), the use of chemical plant protectants went up 30% during the last two decades (FAO, 2022b). Developing and planting biotic-stress-resistant rice cultivars would represent a more effective and sustainable strategy to control biotic stresses in crops. Advances in the understanding of rice innate immunity, including the pathogen-associated molecular patterns (PAMP)-triggered immunity (PTI) and the effector-triggered immunity (ETI), and disease-resistant rice breeding have been previously reviewed from different perspective (Liu & Wang, 2016; J. Yin et al., 2021). Three articles are included in this issue that update our understanding of rice immunity and breeding. Vo et al. (2022) summarized recent advances in the understanding and engineering of ETI in rice, particularly on rice nucleotide-binding and leucine-rich repeat (NLR or NB-LRR) family R proteins and effectors, and proposed promising strategies including using NLRome and Effec-tome studies to overcome challenges and improve rice immunity via engineering ETI (Vo et al., 2022). Zou et al. (2023) characterized functions of an endoplasmic reticulum (ER)-localized ubiquitin-specific protease (UBP), LMM2, in rice cell death and innate immunity. The find that LMM2 can directly interact with SPL35, a coupling of ubiquitin conjugation to ER degradation domain-containing protein that interacts with ubiquitin molecules, and maintain its stability (Zou et al., 2023). Although how SPL35 is ubiquitinated and if ubiquitinated SPL35 is direct de-ubiquitinated by LMM2 is not known, this study provided novel views on rice immunity. Light signalling is known to be associated with plant stress responses. However, its function in rice defense against sheath blight disease is poorly understood. Yuan et al. (2022) presented a more specific story that links light signalling with rice resistance to sheath blight, a major threat to rice production. They found that PhyB inhibits BZR1 (brassinazole resistant 1)-NAC028 (a NAC transcription factor)-CAD8B (cinnamyl alcohol dehydrogenase 8B) signalling and negatively modulates sheath blight resistance in rice; therefore, loss-of-function mutants of *PhyB* are resistant while transgenic plants overexpressing of *PhyB* are sensitive to sheath blight (Yuan et al., 2022).

4 | NATURAL VARIATIONS IN RICE RESILIENCE

The longtime of natural evolution and intense selection during domestication has resulted in tremendous natural sequence variations in rice. Understanding the particularly agronomically-relevant, trait-associated natural variation is crucial for rice breeding to select and combine beneficial variations (Q. Wang et al., 2020). With the rapid advances in whole genome sequencing technology and genome-wide association study (GWAS) analysis, we have witnessed great progress in elucidating the natural variation underpinning agronomic traits and the underlying genetic architectures in rice. For example, *HAN1* (Mao et al., 2019) and *COLD11* (Li, Zhang, Yang, et al., 2022) for chilling tolerance, *OsALs* (Alfin-like family genes) for seed size and drought tolerance (Y. Yang, Ma, et al., 2022), *OsLG3* (an ERF family TF) for drought tolerance (Xiong et al., 2018), *DRO1* for saline tolerance (Kitomi et al., 2020), and *NOMT* (a naringenin 7-O-methyltransferase) for resistant to fungal diseases (Murata et al., 2020). In this issue, Hong, Rosental, et al. (2023) profiled glycerolipids in seeds of 587 Asian cultivated rice accessions and 103 chromosomal segment substitution lines, and revealed their significant natural variation in rice. After mGWAS and mQTL analyses, they revealed that *OsLP1* and *Waxy* are causal genes underlying natural variation in seed-saturated triacylglycerol (TAG) and lysophosphatidylcholine (lyso-PC) contents, respectively. Through combined population genetic analysis, they showed that natural variation in seed glycerolipids has been unconsciously shaped by natural (such as flooding and heading date) and artificial (such as taste) selection (Hong, Rosental, et al., 2023). The analyses of physiological effects of natural variation in seed glycerolipids are still ongoing in this group. Hong, Su, et al. (2023) also performed GWAS on plant height in whole 619 populations and in three *japonica* subpopulations with different *SD1* haplotypes after the effect of *SD1* is fixed, and revealed multifaceted genetic architectures of plant height in rice, and identified two sets of QTL epistatic interactive networks in the subgroup harboring Nipponbare-specific *SD1* haplotype are found to be multieffective QTL/genes, participating as well in flowering, which links plant height QTL/genes with adaptive events such as flowering in *japonica* rice (Hong, Su, et al., 2023), reflecting association of plant height trait with different environmental adaptation events particularly in *japonica* subpopulations.

5 | ROLES FOR HORMONES IN RICE RESILIENCE

Both abiotic and biotic stresses affect homeostasis and signalling of plant hormones. Conversely, plant hormones affect responses of plant to various stressors (Liao & Bassham, 2020). Therefore, altering plant hormone homeostasis and signalling appears promising to enhance the productivity and adaptation, and adoption of stressed crops (Eshed & Lippman, 2019), which

demands a full understanding of the genetic underpinnings plant hormone homeostasis in crops. Song et al. (2022) summarized, in this issue, roles of auxin response factors (ARFs), key components of auxin signalling, in controlling various rice developmental processes including root development, tiller angle, leaf angle, flower organ, and grain size. These authors also introduced auxin response factor-dependent resistance to abiotic (such as heat, drought, flooding, salt and nutrient) and biotic (such as fungi and virus) stresses (Song et al., 2022). Considering OsARFs' essential roles in the regulation of many important agronomic traits and stress adaptation/resistance, the authors suggest that a better architecture and improved resilience in rice is likely to be achieved through genetic engineering of OsARF genes. Chen et al. (2022) reported the role of OsNCED3, an ABA biosynthetic gene, in rice preharvest sprouting resistance and grain development in rice. Overexpression of OsNCED increased the ABA/GA ratio in embryo, enhanced preharvest sprouting resistance, and increased seed size and weight, while knockout of OsNCED did the opposite (Chen et al., 2022). These authors also suggested on the basis of nucleotide diversity analysis that OsNCED is likely selected in *japonica* populations adapting to seed dormancy and germination.

6 | FUTURE OUTLOOK

To secure rice production to meet the demands of an increasing population under changing climates in a sustainable manner, future rice undoubtedly should be environment resilient with moderate response and good performance when grown under stress conditions (Figure 2). Environmental factors are multifaceted, obviously and they have synergistic effects on rice production, at every stage of rice growth and development. Currently, the majority of relevant studies have been carried out on a single stress and under controlled environment conditions, with few on multiple stresses or to some extent under field-based facilities. In addition, molecular responses of rice to environmental factors have been captured mainly in certain tissues at certain specific stages without covering all tissues throughout the whole life cycle. Hence still large gaps exist between theoretical studies and cultivar development, failing to form a virtuous circle for rice breeding. Therefore, new tools and experiment designs are needed to comprehensively elucidate the dynamic nature of rice-environment interaction under real-world grown conditions from the aspect of space and time, to mine and identify key genes or networks/modules, and to lay a solid foundation for breeding environment resilient rice using various strategies and approaches. Special attentions should be paid to the buildup of rice's capacity for balancing stress response and growth & development (Figure 2). Development of DNA markers closely linked to target QTL/genes has made marker-assisted gene pyramiding to combining known agronomic important genes into a single elite genotype in rice more precise and reliable (Haque et al., 2021), the application of marker-assisted breeding to develop stress resilient

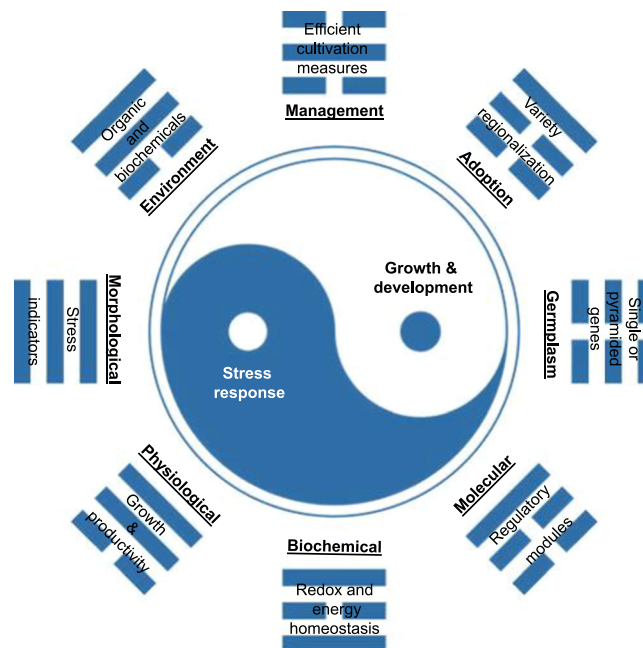


FIGURE 2 Yin-Yang Ba-Gua diagram showing the capacity of balance between stress response (at morphological, physiological, biochemical, and molecular levels) and growth & development (starting from germplasm, passing adoption and management, to environment) in resilient rice grown under stress conditions. [Color figure can be viewed at wileyonlinelibrary.com]

rice varieties based on known genes/QTL for stress resilient and high yield is also promising, although is not straightforward.

Global agriculture consumes 72% of all surface and groundwater resources (FAO, 2021), and global rice production accounts for about 60% of them. To save freshwater resources and reduce paddy field methane emission, future rice should be water-saving and drought-resistant (WDR). Current upland rice is resistant to drought but less productive while lowland rice is sensitive to drought but more productive, due to the genetic trade-offs through tight linkages or pleiotropic effects (Xia et al., 2019). Using conventional pedigree breeding and marker-assisted selection, combined with strong and different types of phenotypic selection for desired yield potential, drought resistance, and water use efficiency, more than 20 new WDR rice cultivars have been developed and grown in China, both in paddy and rain-fed upland, and several varieties have been released to other countries, such as Laos and Bangladesh (Luo et al., 2019). The pyramiding of green characters (such as nutrient efficiency, salt-tolerance, resistance to diseases and insects) in WDR rice, and expansion of WDR development and planting worldwide, offer promises to secure food supply in future.

Both Asian rice and African rice grow annually. However, *O. rufipogon* (the ancestor of Asian rice) is perennial. Due to "one-sow-one-harvest" nature, annual rice is not sustainable in many aspects, and particularly vulnerable to changing climates; Due to a more extensive root systems and greater assimilate reserves, perennial rice can better cope with abiotic stress and grow better in more marginal

landscapes (Zhang, Huang, et al., 2023). Currently three perennial rice cultivars (PR23, PR25, and PR107) produced by crossing of annual Asian rice with its perennial African relative (*O. longistaminata*) have been released in China. A single planting of irrigated perennial rice can be productive for eight consecutive harvests over four years with similar yield of replanted annual rice but much less additional labours, chemicals and seeds (Zhang, Huang, et al., 2023). Perennial rice could be a potential game changer, allowing to supply more rice under changing climates, thus, PR23 was selected as one of the top 10 Science's 2022 Breakthrough of the Year (Pennisi et al., 2022). Introgression of genes encoding biotic stress resistance traits into perennial rice will help to develop perennial rice with both biotic and abiotic resilience.

To improve environmental resilience of cultivated rice, particularly Asian rice, wide hybridization between Asian and African or wild rice could be used, which requires, however, novel techniques besides cytoplasmic male sterile wild rice and embryo rescue. Several strategies are proposed to advance the application of heterosis in rice breeding to further boost yield in future; they include one-line breeding system (through simultaneously knockout four meiosis and fertilization genes), *de novo* domestication of wild allotetraploid rice, and usage of heterosis-associated genes (S. Zhang et al., 2021). Among them, one-line breeding system seems to offer a great promise in a sustainable manner as long as more applicable targets are mined.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable—no new data generated.

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