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REVIEW

Systems-based rice improvement approaches for sustainable food and nutritional security

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Abstract

Key message **An integrated research approach to ensure sustainable rice yield increase of a crop grown by 25% of the world's farmers in 10% of cropland is essential for global food security.**

Abstract Rice, being a global staple crop, feeds about 56% of the world population and sustains 40% of the world's poor. At ~ $200 billion, it also accounts for 13% of the annual crop value. With hunger and malnutrition rampant among the poor, rice research for development is unique in global food and nutrition security. A systems-based, sustainable increase in rice quantity and quality is imperative for environmental and biodiversity benefits. Upstream 'discovery' through biotechnology, midstream 'development' through breeding and agronomy, downstream 'dissemination and deployment' must be 'demand-driven' for 'distinct socio-economic transformational impacts'. Local agro-ecology and livelihood nexus must drive the research agenda for targeted benefits. This necessitates sustained long-term investments by government, non-government and private sectors to secure the future food, nutrition, environment, prosperity and equity status.

Keywords Environmental stresses · Genomic breeding · Nutrient management · Postharvest management · Rice quality · Food security and sustainability

Introduction

Estimates of 60 to 100% higher demand on agricultural products by 2050 compared to 2000 (Alexandratos and Bruinsma 2012) put tremendous pressure on global food security mission. The World Food summit-FAO (1996) stated: "*Food security exists when all people, at all the time, have physical, social, and economic access to sufficient, safe and nutritious food, which meets their dietary needs and food preferences for an active and healthy life*". Enhanced production and productivity of the semi-dwarf, photoperiod-insensitive, fertilizer-responsive, non-lodging wheat and rice varieties produced during the Green Revolution helped avert food shortage in the 1960s (Pingali 2012). Fertilizers, agrochemicals and farm machinery also contributed, but ensuing excessive use of synthetic fertilizers/pesticides adversely affected soil and human health (Pingali 2012). Currently, yield stagnation in 25–40% of the croplands even in agriculturally advanced nations (Ray et al. 2012), decreasing agricultural land area, water and labour issues and postharvest losses aggravate food insufficiency scenarios, all of which aggravate the challenge of feeding ~ 10 billion people by 2050 (Tripathi et al. 2019).

Climate change vagaries further compound agricultural problems. Environmental stresses of heat, cold, drought, flooding and salinity are becoming more severe and frequent. Heat and drought stress decreased cereal production by ~ 6% between 2000 and 2007 (Lesk et al. 2016). Heat stress from rising surface temperature over

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the years will adversely affect plant physiology, development, reproduction and yield (Bailey-Serres et al. 2019). A 1 °C rise in temperature can cause ~ 8% yield loss of milled rice (Lyman et al. 2013). Arable land degradation due to salinity affects ~ 62 Mha (20%) of the world's irrigated lands, corresponding to a loss of ~ $27 billion/annum (https://unu.edu/media-relations/releases/world-losing-2000-hectares-of-farm-soil-daily-to-salt-induced-degradation.html). Salinity in arid and semi-arid farms is due to salt retention after heat-induced evaporation, and in the coastal farmlands due to the incursion of seawater in the deltas due to receding river waters during weak monsoons.

Climate change also influences and aggravates biotic stresses, e.g., bacterial, fungal, viral infections, insect and pest infestation. Worldwide, 25–40% of rice and corn and 10–30% of wheat is lost to plant diseases (Savary et al. 2019). The recent crop and economic losses due to Fall Army Worm infestations, even for *Bt*-corn, illustrate the gravity of the situation (Bengyella et al. 2020). A better understanding of the relationships between biotic stress factors and the climate, and possible remedial solutions are necessary.

Postharvest losses account for significant reductions in the supply chain. About one-third of edible food at the farmgate level is lost annually (1.4 billion tons, ~ USD 1 trillion) due to inadequate postharvest handling and storage (Sawicka 2019). Decreasing postharvest losses would be inseparable from increasing food security (http://www.fao.org/docrep/004/y3557e/y3557e08.htm).

Unsustainable agricultural activity per se causes many problems. Nearly 70% of groundwater withdrawals are for irrigated agriculture (CAST 2019) and water extraction rate exceeding natural replenishment progressively depletes the water table. Expensive water abstraction machinery raises the cost of food and harms the environment by drawing water from deeper sources, further threatening food security (Dalin et al. 2017). Thus, addressing the land, water, labour and postharvest problems under climate change vagaries must include improved agronomic management and best practices. Systems-based landscape level cropping patterns and farm resilience go hand-in-hand with improving crop yield. The balance between intensification and diversification is important for the environment/biodiversity and sustainability. A multifaceted, trans-disciplinary approach for enhancing sustainable food production is necessary (Hellin et al. 2020a) where conventional breeding and agronomy are supported not only by modern genetic engineering and/or genome-scale breeding and precision agriculture technologies, but also by appropriate inputs from socio-economic and policy dimensions (Hellin et al. 2020b).

Rice at the centre stage of global food security efforts

Rice is an important grain crop supporting over half of the world's population. About 85% of rice from ~ 164 Mha is used for human consumption compared to 72% wheat from ~ 214 Mha (http://www.knowledgebank.irri.org/ericeproduction/Importance_of_Rice.htm). Rice is special among cereals because: (a) unlike other cereals it is largely used as grain rather than flour, (b) it is the staple crop of the majority of the poor and hungry population targeted by the global sustainable development goals (http://ricecrp.org/rice-and-the-sdgs/). Millions of small holder and landless farmers rely solely on rice production for their food and livelihood. However, an estimated decline in average rice acreage from 164 Mha in 2017 to 155 Mha by 2050 (Shahbandeh 2019) coupled with estimated yield losses due to biotic/abiotic stresses and post-harvest losses should trigger rapid response alarms.

Rice is second to corn in providing global caloric intake and fourth after corn, wheat, dairy and eggs as a source of protein, because cereals account for the large part of dietary protein intake. Also, rice can grow in the widest range of eco-geographies and environment where other crops cannot (http://ricepedia.org/rice-as-a-crop/where-is-rice-grown). Thus, rice as a source of calories and protein is the bedrock component in a balanced diet for the world's poor. Improving rice quantity and nutritional quality thus promises the easiest route to socio-economic transformation of the vulnerable groups. Over a period of 25 years (1985–2010), improved rice varieties generated through International Rice Research Institute (IRRI)'s efforts amount to a Net Present Value of USD 9.91, 4.27 and 4.85 billion in Indonesia, Philippines and Vietnam, respectively (Brennan and Malabayabas 2011). This substantially improved the status of the extremely poor over the 25 years in these countries, which are now progressive transition economies. Thus, rice must be improved for its nutritional quality to address the double burden of micronutrient deficiency and obesity prevalent in disparate sets of populations in the transition economies.

The looming food crisis driven by demography and climate change can be averted by concerted multidisciplinary research for a pipeline of transforming innovations with socio-economic impacts. Cogently connected up-, mid- and down-stream science of molecular, organismal and topographical considerations, respectively, must be responsive to societal imperatives of prosperity and equity for relevance and value. Most up- and mid-stream plant research never reaches the targeted farmers/customers, and when it does, it is rarely monitored and evaluated for learning and impact on the society. A circular research model starting from socio-economic understanding of climate, market and policy change-based product profile, leading to product development and deployment must end with socio-economic impact assessment.

Using rice as an example we discuss some tested and potential strategies for sustainably enhancing crop productivity and system resilience under the progressively challenging environment. Plant biotechnological and breeding approaches for combating stresses, followed by the role of precision agriculture in water, land, nutrients and postharvest management are considered. The scope to integrate these into landscape-level solutions and facilitate socio-economic transformations is explored. Figure 1 captures a proposed framework where rice research goes all the way from genes and genotypes to potentially influencing policies for clear impact on prosperity, guided by the relevant drivers and enablers.

Sustainable rice yield increase underpins global food and nutritional security

The Green Revolution rice (IR8) and wheat (Rojo64) varieties are archetypical examples of how the breeding of elite crop varieties made a difference (Nelson et al. 2019). There is a rich history of attempts at increasing yield, but not quality. Such increase in grain varieties unwanted by customers is a waste of resources. Hence, increasing yield towards a product profile is now the desirable aim (Custodio et al. 2019). Interfacing conventional and modern approaches is important to fast-track such a process (Kohli et al. 2019) using the following 'breeding by design' approaches.

Conventional hybridization

This time-tested strategy was crucial in developing high yielding rice varieties, but it did not reduce agrochemical and water inputs. Rice varieties released in India between 1974 and 1994 exhibited genetic gain of 1.2% for irrigated rice, but rainfed upland farms on marginal soils registered 1.3% yield decrease (Muralidharan et al. 1996). Conventional breeding is dependent on the available genetic variability, including from the wild relatives. Such efforts resulted in genetic yield increase of 1.9% even under severe reproductive-stage drought in India (Kumar et al. 2021). Breeding for improved submergence tolerance generated 'FR13A' rice, which was 100% tolerant to 7-day complete submergence but had poor agronomic characteristics (Ahmed et al. 2013). 'FR13A' was improved to generate commercially successful varieties 'IR 49,830-7-1-2-2' and 'Sudhir' (Khan et al. 2015). The cloning of *Sub1A* gene resulted in improved mega-variety 'Swarna-Sub1' tolerant to 14 day-submergence (Bailey-Serres et al. 2010).

Ideotype breeding

The rice varieties generated through conventional breeding after 1990 were resistant to many diseases and pests, but lacked grain yield advantage (Muralidharan et al. 2019). Ideotype breeding envisioned modification of the plant

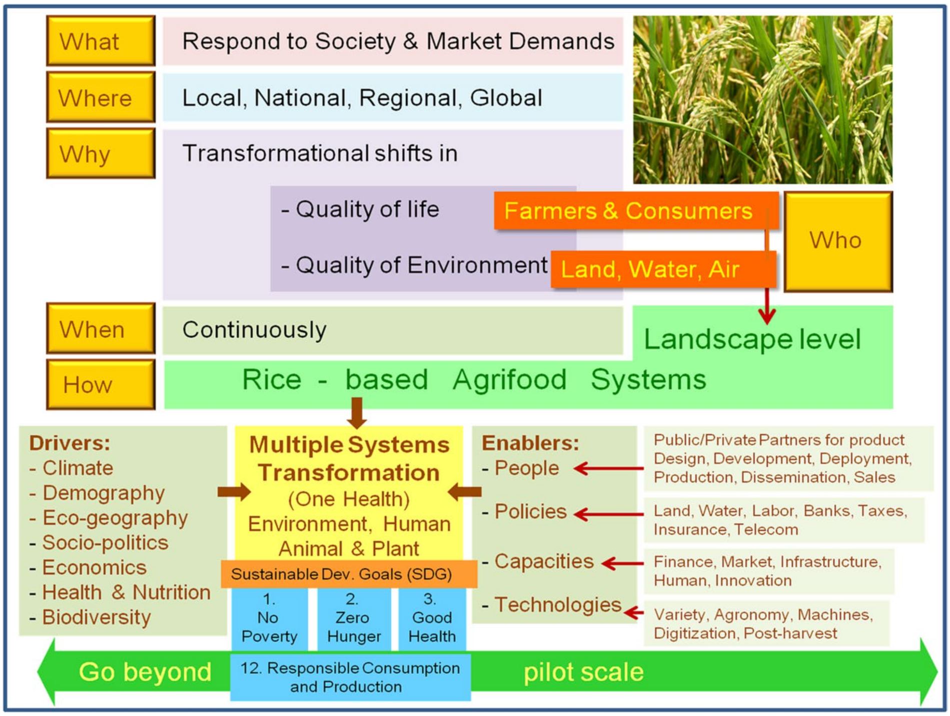

Fig. 1 A proposed framework showcasing how rice-based agrifood systems can help to achieve sustainable developmental goals (SDGs) and bring about transformational shifts in the quality of life and environment. The framework also suggests that rice research can be directed to influence upcoming policies for zero hunger and good health

architecture to enhance yield. Yield improved because of decreased lodging in 'IR8' rice (Nelson et al. 2019). The 'New Plant Type (NPT)' envisioned 200–250 grains/panicle, without unproductive tillers or unfilled lower spikelets (Khush 2013). However, its grain quality was inferior and hence, the product undesirable. Marketable grain quality must always accompany yield increase. China's 'super' rice exemplifies ideotype breeding, where the F1 hybrid varieties are a combination of ideotype and intersubspecific heterosis (Peng et al. 2008; Yuan 2017). The hybrid had NPT features, namely, increased grain numbers, reduced tillering and improved lodging resistance. Further improvement was made by achieving the top three leaves of the canopy, instead of the lone flag leaf, to supply increased photosynthates to the large panicles (Peng et al. 2008). Taken together, the NPT and 'super' rice exemplified that ideotype breeding could break yield barriers.

Molecular breeding

The advent of molecular technologies and PCR in the 1980s improved on older tools, e.g., restriction fragment length polymorphism and led to several PCR-based markers that were used to trace genomic segments relevant to crop improvement. Subsequently, genome sequencing led to identifying numerous DNA-based markers for marker-assisted selection (MAS). This helped in screening for difficult, expensive or time-consuming traits at any growth stage while distinguishing heterozygotes. Molecular markers served to understand polygenic traits with quantitative trait loci (QTLs). The merger of MAS with QTLs contributed significantly towards boosting yield (Segami et al. 2016) and improving the nutritional quality of rice (Mahender et al. 2016). QTLs are known for yield component traits, e.g., panicles/plant, grains/panicle and grain weight. For panicle number QTLs *pn4*, *pn6* (Rahman et al. 2008) and *qPN2* were identified from an eight-way multi-parent advanced generation intercross (MAGIC) population (Meng et al. 2016). Introduction of *GW6* to *indica* variety 'HJX74' caused 10.44% yield increase by promoting grain width and weight (Shi et al. 2020). In most studies, information on grain quality was missing. Recently, a gene has been identified that increases secondary branches in the upper parts of the panicle, generating more filled spikelets, and thus increasing the yield of good quality grains (Pasion et al. 2021).

Pyramiding of QTLs or their causative genes in a single elite cultivar can integrate multiple traits. Pyramiding *sd1* (semi-dwarf gene), *Sub1A* (submergence tolerance), *Pi9* (blast resistance) and *Xa21* and *Xa27* (bacterial blight resistance) in 'Khao Dwak Mali 105', an elite Thai aromatic rice, led to semi-dwarf, lodging- and submergence-tolerant plants (Luo and Yin 2013). The semi-dwarf, biotic and abiotic stress tolerant aromatic 'Temasek Rice' variety requires low inputs, which further exemplifies the gene pyramiding power of MAS (http://www.tlv.sg/news/singapore%E2%80%99s-temasek-rice-developed-by-tll-scientists-for-regional-food-security/).

Genomic breeding

Use of very high-density MAS underpins breeding by genomic selection (GS). Data correlating high-throughput genotyping and phenotyping on a test population are used by computer models to predict performance from the genotype. Multitude of DNA markers define a genotype and a combination of markers can predict the performance of traits. Low coverage sequencing of a large number of rice accessions can feed the GS models for increased prediction accuracy on the performance of individuals from biparental or multiparental populations. GS is useful for complex traits controlled by multiple genes and its prediction accuracy saves time and resources spent on phenotyping. Different prediction models can be tested and the most effective one identified for improving a complex trait, e.g., for rice blast disease resistance. Combining the GS approach with genome-wide association studies (GWAS) was shown to be more effective and such GS models work better for some traits (Spindel et al. 2015).

Genetic engineering

The availability of genome sequences and efficient functional genomics tools, including insertion mutagenesis and genome-wide expression profiling have helped identify candidate genes for crop improvement. Biswal et al. (2017) provide details of rice crop improvement by overexpression or silencing of many genes. *High Mobility GroupB* (*HMGB*) genes were identified from rice (Wu et al. 2003a, b), and overexpression of this class of genes conferred stress tolerance to Arabidopsis (Kwak et al. 2007). The 'Golden Rice' project shows how biofortification of rice with β-carotene by genetic engineering can prevent Vitamin A deficiency aimed at preventing blindness in children (http://www.goldenrice.org/). Similarly, Fe-biofortified 'IR64' rice with 15 µg/g Fe in polished grain has been generated (Trijatmiko et al. 2016). Genetic engineering approaches have also been exploited for manipulating plant architecture for improving rice crop yield. RNAi-mediated suppression of *OsPIN5b*, an auxin carrier protein, leads to pleiotropic effects, such as, higher tiller number, longer panicles and higher grain yield (Lu et al. 2015). A recent review has highlighted modulation of miRNAs as a potential genetic engineering tool for enhancing rice yield by manipulation of plant architecture (Kaur et al. 2020). The recent approval for cultivation of the Golden Rice in the Philippines and its prior approval for consumption in Australia, Canada and New Zealand are encouraging for the appropriate use of GM tools for rice crop improvement. Collectively, these examples highlight the potential contribution of genetic engineering in identifying new gene families and utilizing them for rice improvement.

Genome editing

This technique exploits site-specific nucleases (SSNs) to precisely add, delete or substitute DNA bases in selected genes. The SSNs include zinc finger nucleases (ZFNs), transcriptional activator-like effector nucleases (TALENs) and clustered regularly interspaced short palindromic repeats (CRISPR)-associated endonuclease Cas9 (CRISPR/Cas9; Manghwar et al. 2019). Identification of CRISPR/*Cpf1* has opened up new avenues for genome editing because of its better DNA cleavage efficiency over CRISPR/Cas9 (Zetsche et al. 2015). Base editor technology that enables direct conversion of target bases without the need for DNA-strand break has been developed (Komor et al. 2016). CRISPR/Cas9 tool has broadened the horizon of rice yield improvement programs. Knocking out genes that limit yield and quality parameters, e.g., *GS3*, *DEP1* and *Gn1a* caused significant increase in rice production with plants having dense erect panicles, larger grains, and enhanced grain number (Li et al. 2016). The editing tool also enables pyramiding null mutants in a single cultivar. Simultaneous mutation of *GW2*, *GW5* and *TGW6* (triple null) using CRISPR/Cas9 editing caused 29.3% increase in grain weight (Xu et al. 2016). CRISPR/Cas9 is being used to generate large-scale rice mutant libraries for functional genomics and genetic improvement (Meng et al. 2017).

A systems approach in up-, mid- and down-stream science is essential for impact

Designing effective projects depends on streamlining the upstream discovery component for proof-of-concept to mid-stream validation of a scaled model, downstream deployment and final impact assessment. The discovery component is facilitated by molecular data such as genome sequences, and integrative science such as understanding photosynthesis in terms of optimal water and assimilate utilization.

Upstream discovery science

The 3000 rice genome project

The genomic information gathered so far has helped to identify numerous genes to challenge the existing yield barriers. Transgenic rice lines generally stop at functional validation due to the tough regulatory barriers, limiting their commercialization. However, superior alleles can be discovered from a wider gene pool, and after transgenic validation, be used in conventional breeding to introgress the trait to the desired elite background. To harness the vast genetic diversity available within wild and domesticated rice, IRRI, the Chinese Academy of Agricultural Sciences and Beijing Genomics Institute sequenced over 3000 rice genomes (3K-RGP 2014). Molecular breeders and genetic engineers can use the generated sequence data, single nucleotide polymorphisms (SNP) and structural variations—deletions, duplications, inversions and translocations—among the 3010 rice genomes (Wang et al. 2018). Using the 3K-RGP information, tight linkage between semi-dwarf mutant gene, *sd1* and drought susceptibility genes was discovered in all semi-dwarf varieties, and the linkage could be broken in some naturally occurring or breeding lines (Vikram et al. 2015).

Enhancing photosynthetic efficiency

Photosynthesis is the primary determinant of plant growth, development and yield. Genetic manipulation to enhance photosynthesis has been attempted in three processes: photosynthetic efficiency, photorespiration, and electron transport. Photorespiration was targeted because it decreases carbon assimilation (Walker et al. 2016a, b) and the GOC bypass (named for three enzymes: glycolate oxidase, oxalate oxidase, catalase) was established in rice chloroplast using a multi-gene assembly, which resulted in improved characteristics (Table 1). Photosystem components, including electron transport system (Table 1; Ramamoorthy et al. 2018; Zulfugarov et al. 2014) and biophysical CO_2 concentrating mechanisms (CCM) have been genetically modified. Rubisco converts nearly 90% carbon into biomass but its slow catalytic rate and competing oxygenation reaction are limiting factors for carbon fixation (Erb and Zarzycki 2018). In cyanobacteria and algae, conversion of bicarbonate into CO_2 occurs in a compartment to increase the CO_2 available for Rubisco. Similarly, C4-plants possess a CCM to enrich CO_2 around Rubisco (Karki et al. 2013). Computational modeling and transgenesis in model plants suggested prospects of engineering algal CCM in rice (Table 1). Accordingly, the C4 rice project aims to generate varieties possessing C4 photosynthesis (Ermakova et al. 2020; Karki et al. 2013; Nomura et al. 2005). Since the inception of the international C_4 rice consortium in 2008, substantial progress has been made in identifying several unknown components of C_4 biochemistry. An important contribution of the consortium includes the transcriptomes of bundle sheath and mesophyll cells of multiple C_3 and C_4 plant species (Schuler et al. 2016). The data helped to identify putative candidate genes with their cell-type specific expressions and metabolite shuttling between the two cell types. However, some of the key aspects, such as, photosynthetic functionalization of

Table 1 List of potential target genes for manipulating photosynthesis in rice & proposed strategies for engineering CCM

Targeting photosynthesis

	Target	Gene involved	Manipulation	Biochemical effect	Growth, biomass yield and others	Comments	References
1.	Calvin cycle	Sedoheptulose-1,7-bisphosphatase (SBPase)	Constitutive expression	Increase in SBPase activities Increased CO2 assimilation rates Enhanced photosynthesis	Higher growth rate Enhanced salt tolerance	SBPase regulate rubisco activation by more regeneration of ribulose-1,5-bisphosphate in the soluble stroma	Nomura et al. (2005)
2.	Calvin cycle	Transketolase	Co-overexpression with rubisco	Increase in transketolase content	No significant changes to biomass and other agronomic traits	Transketolase might not a limiting factor of photosynthesis	Ermakova et al. (2020)
3.	Calvin cycle regulation	Rubisco Activase (Rca)	Tissue-specific expression of barley and maize Rca	Reduction in Rubisco level Enhanced non-steady state photosynthesis upon light induction	No detrimental effect on growth and yield	Barley and maize Rubisco Activase can mediate and enhance enhance Rubisco activation in rice	Feng et al. (2007); Suzuki et al. (2017)
4.	Photorespiration	Glycolate oxidase (OsGLO3), oxalate oxidase (OsOXO3), and catalase (OsCATC).	Simultaneously expression of three enzymes (OsGLO3, OsCATC, and OsOXO3) and directed into chloroplasts	Elevated amounts of glucose, fructose, and sucrose lower ratios of glycine/serine	Enhanced photosynthetic efficiency, Iincrease in overall yield, Increase in nitrogen content In the field condition	Photorespiratory Bypass in Rice Chloroplasts	Lakshmanan et al. (2013); Yamori et al. (2012)
5.	Electron transport	Chloroplast gene psbA (D1 subunit of photosystem II)	Allotropic expression of the psbA by a heat-responsive promoter	Enhanced D1 level Improves the repair of photosystem II.	Enhanced plant heat tolerance Increased CO2 assimilation rate Increased biomass and grain yield	Strategy to get enhanced crop yield under normal as well as heat-stress conditions	Jan et al. (2013)

Proposed strategies for engineering CCM into rice

Origin	Component involved	Proposed mechanism	Early progress	References
Cyanobacteria	HCO3− Transport System	Installing a cyanobacterial HCO3− transporter at the chloroplast inner envelope membrane (IEM)	Computational model suggested that introduction HCO3− transporter could lead to up to 16% increase in CO2	Fukayama et al. (2012); Shen et al. (2019)
Cyanobacteria	Synthetic Carboxysomes	Building functional carboxysomes in plant cells along with with efforts to target cyanobacterial HCO3− transporters	α-carboxysome has been assembled in E. coli minimal α-carboxysome-like structures has been reconstituted in tobacco	Price et al. (2011); McGrath et al. (2014)
Eukaryotic algae (Chlamydomonas reinhardtii)	Pyrenoid (non-membrane-bound organelle within the chloroplast of eukaryotic algae, where Rubisco is clustered)	Reconstituting a pyrenoid in crop plant	Expression of several key components of chlamydomonas CCM have been tested in model plants.	Karki et al. (2013); Long et al. (2018)

the bundle sheath still remains an important step for C_4 rice development (Ermakova et al. 2020). Greater ATP requirement for C_4 photosynthesis is another challenge that needs to be addressed to achieve C_4 rice. Contemporary successes in manipulating photosynthesis were contextualized for their downstream socio-economic impacts (Kohli et al. 2020). Parallel research on nutrient and water use efficiencies is recommended, e.g., how stomatal density promotes photosynthesis, water use efficiency and drought tolerance.

Combating biotic stresses

Annually 25 to 40% of rice is lost to pests and diseases (Sparks et al. 2012). Fungal blast caused by *Mangaporthe oryzae* and bacterial leaf blight caused by *Xanthomonas oryzae* pv *oryzae* (*Xoo*) severely reduce rice yield. Genetic analyses identified more than 100 genes conferring resistance to *M. oryzae* (Sharma 2012). Resistant lines were developed by introgressing blast resistance genes *Piz-5* and *Pi-54* into Basmati rice restorer line 'PRR78' (Singh et al. 2013). Furthermore, blight (*Xa-13, Xa-21*) and blast (*Pi-54, Pi-1*) resistance genes were pyramided into the mega-variety 'Tellahamsa' conferring resistance against both pathogens (Jamaloddin et al. 2020). *Xoo* acts by secreting transcription-activator-like effectors that bind to specific promoter sequences and induce sucrose transporter (*SWEET*) genes. This host susceptibility function was blocked by CRISPR/Cas9 editing of five *SWEET* gene-promoters in 'Kitaake' rice resulting in robust broad-spectrum resistance against *Xoo* (Oliva et al. 2019). New genetic tools, e.g., small interfering RNA and host-induced gene silencing have also been utilized (Guo et al. 2019).

Brown planthopper (BPH) also affects rice crop substantially by feeding inside the panicle stalk causing unfilled grains called "white heads". Several QTLs and genes for BPH resistance are known. Constitutive expression of *Bacillus thuringiensis* genes [*cryIA(b), cryIA(c)*] increased BPH-resistance without yield penalty (Tu et al. 2000). Ideally, lines with multiple stress tolerance/resistance without yield penalty can be achieved by introgressing multiple polygenic traits governed by QTLs, a challenging but possible approach being attempted by refining the marker technologies (Platten et al. 2019). Table 2 lists some genes that regulate abiotic stress tolerance and grain yield that may be used to drive future crop improvement strategies.

Combating abiotic stresses

Abiotic stress tolerance can rarely be treated as a single trait unlike biotic stresses. Thus, heat stress accompanies drought, salinity causes physiological dehydration, drought exacerbates nutrient stress, flooding imparts oxygen and nutrient stresses, and redox stress accompanies most stresses. Due to such complex polygenic control of tolerance, QTLs are at the forefront of effective solutions, e.g., *Saltol* for Na^+/K^+ ratio (Gregorio 1997) conferring salinity tolerance to seedlings. Genetic engineering approaches have also played an important role in improving the abiotic stress tolerance of rice. Rice plants overexpressing *OsDREB* transcription factors showed enhanced tolerance to salinity stress (Mallikarjuna et al. 2011). Similarly, overexpression of *OsSAPK4* accumulates less Na^+ and Cl^- and shows improved photosynthesis (Diedhiou et al. 2008). Other genes for salt tolerance in rice (Hoang et al. 2016) include, *NHX1* from the mangrove *Avicennia officinalis* (Krishnamurthy et al. 2019), *OsTPS8* (Vishal et al. 2019) and *OsCYP94B1* from rice (Krishnamurthy et al. 2020).

A large effect QTL (LEQ) *qDTY12.1* explained nearly 51% of the genetic variance for grain yield under drought (Dixit et al. 2015). The need for the entire QTL containing multiple genes to confer stress tolerance provided a mechanistic explanation, which was supported by proteomic and metabolomic studies on *qDTY12.1* (Raorane et al. 2015a, b). For drought stress, transcription factors and genes targeting root morphology and root system architecture have also been considered (Biswal et al. 2017).

Engineering of *OsRR22* by CRISPR/Cas9 led to significantly high salinity tolerance at the seedling stage (Zhang et al. 2019). Development of mutant alleles of *drought and salt tolerance* (*DST*) by CRISPR/Cas9 editing in 'MTU1010' *indica* cultivar also resulted in moderate tolerance to osmotic stress and high tolerance to salt stress (Kumar et al. 2020). Adaptation to low temperature has also been achieved by editing *TIFY1a* and *1b* genes (Huang et al. 2017). CRISPR/Cas9-mediated knockout of *osmotic stress/ABA-activated protein kinase 2*, *OsSAPK2*, revealed a critical role of *OsSAPK2* in ABA signalling cascade and hence, in abiotic stress tolerance, as the mutant plants were susceptible to stress conditions (Lou et al. 2017). CRISPR/Cas9 also improves abiotic stress tolerance by knocking out transcription factors negatively regulating tolerance-responsive genes. The knockout of R2R3-type *OsMYB30* by CRISPR/Cas9 increased grain yield and cold tolerance in mutant as compared to wild-type rice plants (Zeng et al. 2020). Identification and functional characterization of these and other such genes will help in gene editing for rice crop improvement.

Manipulating hormonal signalling

Advances in the knowledge of genetic networks underpinning hormone signalling pathways have also played a vital role in improving our understanding of abiotic and biotic stress responses (Hoang et al. 2016; Kumar 2013; Verma et al. 2016). Different plant hormones function independently as well as with complex signal interactions to

Table 2 Gene families regulating abiotic stress tolerance and agronomic traits in rice

Gene families regulating salt tolerance and agronomic traits in rice and other plant species

S. No.	Family/Group	Gene	Overexpression/ down-regulation/ mutant	Altered growth and /or agronomic traits	Abiotic stress tolerance	Process(es) involved	References
1.	*CYP714*	*PtCYP714A3*	Ectopic expression of *PtCYP714A3* in rice	Semi-dwarf, increased tillering and reduced seed size.	Salinity tolerance	Na+ and K+ homoeostasis, Gibberellins (GAs) signaling (GA biosynthesis genes were significantly reduced)	Guo et al. (2013)
2.	*OsRLCK* (Receptor-Like Cytoplasmic Kinase)	*STRK1*	STRK1 overexpression	Improved growth at the seedling stage and limited the grain yield loss under salinity stress	Salinity and oxidative stress tolerance	Higher catalase activity and lower accumulation of H2O2 by by phosphorylating and activating, catalase CatC	You et al. (2014)
3.	CCCH-type zinc finger	*OsTZF1*	*Ubi:OsTZF1* *OsTZF1*-RNAi	Retardation of seed germination and seedling growth as well as leaf senescence was delayed Opposite of *Ubi:OsTZF1* phenotype	Salinity tolerance Salt sensitivity	ROS (reactive oxygen species)	Miura et al. (2010)
4.	TPS family	*OsTPS8*	Overexpression	No detrimental effect on any of the agronomic traits	Salinity tolerance	Enhancing suberin deposition, altered soluble sugar level and ABA signaling	Wang et al. (2016)
5.	Photosystem II	Chloroplast gene psbA (D1 subunit of photosystem II)	Allotropic expression of the psbA under heat-responsive promoter	Enhanced biomass and grain yield	Heat stress tolerance	Improves the repair of photosystem II.	Jan et al. (2013)

stimulate an effective response against the different stresses faced. One of the earlier findings exhibiting significant reduction of endogenous bioactive GAs in response to salinity stress provided a vital breakthrough about the integral role of plant hormones in ameliorating stress responses (Achard et al. 2006). GA biosynthetic mutant, *ga1-3*, also showed enhanced survival in salt stress conditions. GA signalling also impacts reactive oxygen species (ROS) levels, as DELLA proteins, the negative regulators of GA signalling, stimulate the expression of genes encoding ROS detoxification enzymes (Achard et al. 2008). More recently, it has been shown that GA can rescue seed germination in mutant rice line with impaired brassinosteroid signalling that otherwise fails to initiate seed germination (Li et al. 2020).

With the genomic information, we now know that the breeding efforts that led to the successful Green Revolution rice variety 'IR8' arose from inadvertent loss of function of *SD1* gene. *SD1* encoded a key enzyme GA20 oxidase necessary for gibberellin (GA) biosynthesis, and the plants with this mutation have reduced amount of bioactive GA leading to semi-dwarf phenotype (Ashikari et al. 2002). The DELLA family of GA signalling intermediates consists of five members in Arabidopsis and two genes in corn. However, based on the constitutive GA response phenotype of *slr1* mutants, there appears to be only one member of the DELLA family in rice, namely, SLR1 (SLENDER RICE 1). Additionally, two sequences homologous to SLR1: SLR1-like1 and -2 (SLRL1, SLR2) have been identified in rice genome databases. Although SLRL1 and SLRL2 contain regions with high similarity to the C-terminal conserved domains in SLR1, they lack the N-terminal conserved region of the DELLA proteins. Transgenic rice plants overexpressing SLRL1 or SLRL2 also exhibited a GA-insensitive dwarf phenotype, indicating that the proteins may function as repressors of GA signalling (Liu et al. 2007; Itoh et al. 2005). These findings suggest that GA signalling pathway intermediates are prime candidates for crop breeding to modify plant height.

Auxins, another major developmental hormone, are also modulated by salinity stress as the stress influences the growth and direction of root growth. About 31 *OsIAA* genes, genes encoding repressors of auxin signalling, and 25 *OsARF* genes, genes encoding transcriptional activators of auxin signalling, in rice were found to be induced by salinity stress (as well as in drought; Song et al. 2009). The activation of *OsPIN3t*, the auxin transporter, providing drought tolerance to rice plants and its knockdown resulting in crown root abnormalities at the seedling stage also offered a strong piece of support to the role of auxin signalling in abiotic stress responses (Zhang et al. 2012).

Cytokinins, generally known for stimulating cell division and differentiation, are also found to be linked to different abiotic stresses. Plants that overexpress *Cytokinin oxidase* (*CKX*) exhibited higher tolerance to drought stress (Werner et al. 2010), a phenomenon also shown by mutants having decreased cytokinin content. On the contrary, another study showed that expression of the cytokinin biosynthetic gene, *Isopentenyltransferase* (*IPT*), also resulted in enhanced drought tolerance in rice (Peleg et al. 2011). This signifies that both increase and decrease of endogenous cytokinin levels and possibly their signalling intermediates should be explored in efforts to improve stress tolerance in plants.

Abscisic acid (ABA) is known as the "stress hormone" as it is one of the most important messengers in facilitating adaptation of plants to different abiotic stresses. ABA regulates the expression of a myriad of stress-responsive genes including dehydrins, *LEA* and those responsible for the accumulation of compatible osmolytes. Overexpression of rice ABA receptors was also able to improve drought tolerance by activating stress-responsive genes (Kim et al. 2014). The importance of ABA is evident from the study involving overexpression of ABA biosynthetic gene *9-cis-epoxycarotenoid dioxygenase* (*NCED*), which causes an increase in endogenous ABA levels with corresponding reduction in stomatal density and elevated drought tolerance in transgenic Arabidopsis plants (Iuchi et al. 2001). In Arabidopsis the stomatal development is known to be regulated by several bHLH transcription factors, namely, SPEECHLESS (SPCH), MUTE, FAMA, and SCREAM (SCRM) and SCRM2 (Lau et al. 2014; Buckley et al. 2020). The feasibility of modifying genetic mechanisms associated with this developmental pathway along with some of the lesser-known genes such as SCARECROW, SHORTROOT and selected Cyclin-Dependent-Kinases has been discussed for improving drought tolerance in rice and other monocotyledons (Buckley et al. 2020).

Besides the major plant hormones mentioned above, jasmonic acid (JA), salicylic acid (SA) and ethylene (ET) also play crucial roles in regulating plant abiotic stress responses. Overexpression of Ethylene Response Factors (ERFs), considered as the effectors of ET signalling, exhibited enhanced drought tolerance, owing to the expression of stress-responsive genes including proline biosynthesis (Zhang et al. 2010). JA levels were also found to be upregulated in the roots and leaves of rice plants in response to drought and salinity stress conditions (Kiribuchi et al. 2004). Similarly, a vital SA biosynthetic enzyme was induced upon salt stress resulting in enhanced SA levels in rice seedlings (Sawada et al. 2006). Taken together, it is evident that phytohormone signalling pathways can be effectively engineered to develop stress-tolerant crops without severe yield penalties. However, more extensive work is required to completely harness the underlying potential. A key aspect that requires intensive focus is hormonal crosstalk, because, hormones are known to function in a synergistic mode, rather than acting independently.

Midstream crop and resource management science

Applying water conservation approaches

The amount of water used in rice cultivation, which is almost 50% of all agricultural irrigation, must be reduced. In one approach called Alternate Wetting and Drying (AWD), fields are subjected to intermittent rather than continuous flooding (http://www.knowledgebank.irri.org/training/fact-sheets/water-management/saving-water-alternate-wetting-drying-awd). AWD reduces 20–30% water, reduces methane and nitrous oxide emissions and improves soil quality and fertility by helping the absorption of zinc and nitrogen (Allen and Sander 2019). System of Rice Intensification (SRI) is another technology that improves water use efficiency by promoting larger root system and better root biota, thereby providing additional environmental benefits (https://www.echonet.org/the-echo-update-blog/2013/7/10/improved-rice-production-system-of-rice-intensification).

Improved cropping system management

Intensive farming with poor crop management practices has led to loss of soil fertility and nutrient deficiencies. Diversification is key to sustain rice productivity. Rice rotation with legumes/pulses is a highly productive cropping system. It is good for biological nitrogen fixation; reduction of disease, pest and weed incidence; provides protein-rich food and feed; and improves profitability as cash crops. The choice of the alternative crop (legumes, oilseeds, manure/feed) is critical and based on location, environment and synergism for higher productivity and efficient resource utilization.

Zero-tillage, a resource-conserving technology, has emerged as a key practice for improving productivity and food security while benefiting the environment (http://www.knowledgebank.irri.org/images/docs/reduced-and-zero-tillage-options.pdf). Crops are grown without tilling the soil, resulting in less greenhouse gas emission because of avoiding straw burning. The simplest zero tillage uses soil moisture and surface seeding without land preparation (http://www.knowledgebank.irri.org/images/docs/reduced-and-zero-tillage-options.pdf). It is preferred in non-puddled, dry direct-seeded rice (DSR) and overcomes water and labour shortage. IRRI has started DSR breeding program to address issues that limit DSR success, including weeds, nematodes, iron toxicity and mechanization.

Furthermore, parallel use of organic manures, e.g., farmyard manure (FYM) that is rich in nitrogen and other organic residues, can help to moderate the use of chemical fertilizers. Using the fallow periods for fast-growing green manures before rice transplantation also reduces nitrogen requirement by improving the soil and reducing leaching and denitrification (Sravan and Murthy 2014). Since 25% of nitrogen, 50% of phosphorus and 75% of potassium are retained in crop residues (Sravan and Murthy 2018), they are excellent for increasing soil organic content. Use of green manures also increases soil pore space. SRI combined with organic manures gives significantly higher yield compared to conventional fertilizers (Harikesh and Kumar 2018). Monitoring soil health via ‘soil health-card system’ that records various quality parameters, can better help to manage soil by replenishing only the depleted nutrients (Sravan and Murthy 2018).

Minimizing postharvest losses

Postharvest losses (PHL) account for the loss of nearly one-third of agricultural production globally (1.3 billion ton; Mopera 2016). For rice, PHL range between 15 and 25% in Southeast Asia (Gummert 2013). PHL occur all along the supply chain and include losses due to spoilage. Rice is more vulnerable to PHL in developing nations due to inadequate/inefficient technology, poor storage infrastructure and improper handling. Although grain loss occurs at harvesting, threshing, winnowing, and transportation, maximum loss happens during storage because traditional storage structures have high moisture levels inviting pests, pathogens and rodents. Fungal infection during storage leading to mycotoxin contamination, grain shattering during harvest and lack of accessible milling facilities add to PHL. Technologies such as fumigation and use of storage insecticides and pesticides can significantly reduce PHL. Synthetic insecticides, such as, methyl bromide and phosphine and plant-based chemicals, such as, leaves and oil extract of *Chenopodium ambrosioides* are effective in minimizing pest infestation. Lastly, airtight storage is useful in avoiding storage losses and chemical or pesticide use. Despite such importance, PHL has not received adequate attention. While food security efforts have focussed on improving rice production, mitigating PHL can significantly impact rice availability.

Downstream demand, deployment and distinction analysis

Meeting demand for nutritional rice

Rice improvement for nutritional security is a critical component of an integrated and holistic view on food security. Despite being seen as a nutritionally poor starch-rich food (largely due to generating polished white grains that are easily digestible, organoleptic grains), rice is rather rich in primary and secondary metabolites of nutritional value (Lee et al. 2019). Coloured or brown rice, partial milling, parboiling and germination-initiated rice are some routes to harness the innate and diverse nutritional attributes of different rice sub-types. To address micronutrient deficiency, especially for zinc, whose lack is critically associated with stunting in children, the mainstreaming of increased zinc in the breeding pipeline has been adopted (Swamy et al. 2016, 2018). Grain iron and zinc were increased in transgenic plants to useful levels for ameliorating micronutrient deficiency (Ludwig and Slamet-Loedin 2019). A recent report demonstrated that reduction of phytic acid content by RNAi-mediated silencing of multifunctional *OsITPK5/6K-1*, a major inositol triphosphate kinase (*ITPK*) homolog involved in phytic acid biosynthesis, is another approach for increasing iron and zinc content in the grain endosperm (Karmakar et al. 2020). The validity of increasing Vitamin A in the 'Golden Rice' grains is now well known and detailed characterization and safety assessment have been conducted (Swamy et al. 2019). Besides improving micronutrient and vitamin contents, there is also substantial progress in generating rice lines with low glycemic index (GI), as high GI is often considered unhealthy. Attempts have also been made to increase the lysine content of rice, as lysine is a limiting essential amino acid in rice. Expression of *Lysine-Rich Protein* (*LRP*) gene under endosperm-specific *Glutelin1* (*GT1*) promoter increased lysine content in transgenic rice seeds by more than 30% (Liu et al. 2016). Additional quality traits of head rice recovery (HRR) during milling (Butardo and Sreenivasulu 2019), chalkiness (Santos et al. 2019), dietary fibre (Kosik et al. 2020), cooking traits (Misra et al. 2018) and secondary metabolites (Llorente et al. 2019) are also being actively addressed. CRISPR/Cas9 was used in improving the nutritional quotient of rice grains by targeting two rice starch branching enzymes *SBEI* and *SBEIIb*, with *sbeII* mutant showing significant increase in amylose and resistant starch content, which helps prevent diabetes (Sun et al. 2017).

Deployment of improved production systems

Demography and climate change call for improved production systems. Innovations to cope with climate change are clubbed under climate-smart agriculture (CSA). Three principles define CSA: (1) increasing agricultural productivity to support increased incomes, food security and development; (2) increasing adaptive capacity and resilience to climate variability at multiple levels (from farm to nation); (3) decreasing greenhouse gas emissions where possible and

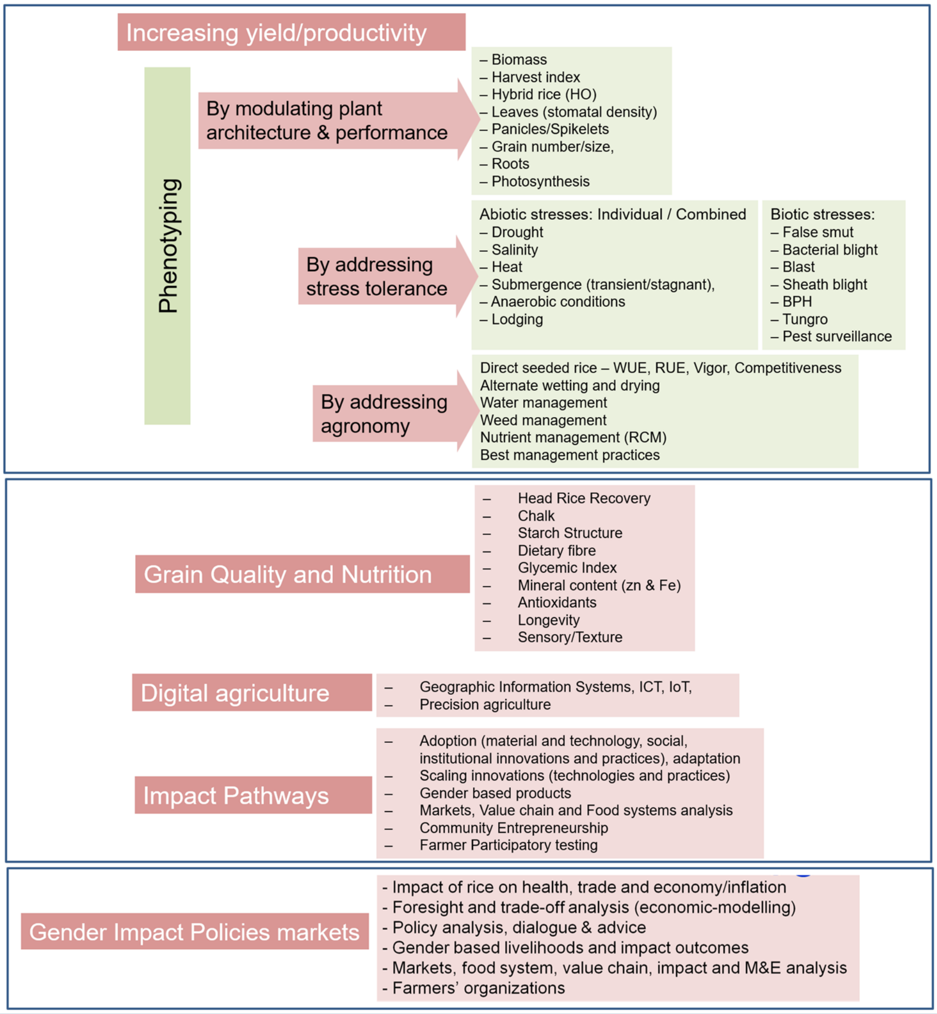

Fig. 2 The components of a multi-disciplinary systems approach required for improving rice yield and quality and increasing its influence on policies and markets. Introduction of gender-based products and scaling of innovative technologies can further extend the boundaries

appropriate (Douthwaite et al. 2017). A sustainable increase in crop yield will spare the natural resources, including land, from agriculture (Phalan et al. 2016), allowing more biodiversity and affiliated land use that restore natural surroundings. Improved crop resilience can also lead to yield gains even with low investment by farmers with smaller land holdings, thereby resulting in increased incomes and social and economic security. Decreasing greenhouse gas emissions, particularly methane from inundated paddy fields will also have a significant impact on natural ecosystems. Globally, rice production fields emit about the same amount of greenhouse gases as Germany. Simple practices, such as, AWD, DSR and rice straw management can lower methane emissions by up to 70%. The challenges calling for CSA are extremely complex and they can be best addressed through trans-disciplinary professionals involving researchers, extension workers and policy specialists (Hellin et al. 2020b). Therefore, agricultural research must be integrated into a systems approach involving agronomists, environmental scientists and socio-economists along with plant breeders, geneticists and agricultural extension efforts. Figure 2 captures the major research areas that illustrate trans-disciplinarity. A new global consortium the "Sustainable Rice Landscapes Initiative" (https://www.unenvironment.org/news-and-stories/press-release/new-consortium-reduce-environmental-footprint-rice-production) will bring experts from research institutions, international organizations and influential business groups on a common platform to reduce the environmental footprint of rice production. The consortium aims to facilitate policy support from governments along with technical training.

Concluding remarks and future directions

Despite being extensively studied in the last few decades, rice still has tremendous research scope. This is because it is eco-geographically most spread out and hence, the findings from one eco-geography may not hold in another. Hence, increased research investment in rice will address the socio-economic as well as the wide ranging eco-geographic diversities. A significant amount of resource allocation right at the upstream level will facilitate innovation at the core of the delivery pipeline. Moreover, the availability of vast amounts of genetic and genomic information, coupled with the rapid upsurge in the development of omics technologies at various levels, such as, genomes, epigenomes, transcriptomes, epitranscriptomes and proteomes will also contribute to the development of newer strategies for crop variety development. This ensures that the daunting task of maintaining food supply in the face of climate change can be accomplished. However, this would also entail institutional-level support by formulation of policies for fast-tracking delivery processes. For example, "seeds without borders" (https://www.irri.org/news-and-events/news/agreement-multi-country-seed-sharing-reached) espouses the cause that seeds of new varieties tested in a particular eco-geography should be available to countries with similar eco-geographies without the political blocks and time spent in re-testing within country boundaries.

It is imperative that innovation at all levels must be assessed for scientific as well as socio-economic relevance through the stage-gating progress. This would enable only the most impacting undertakings to proceed through the

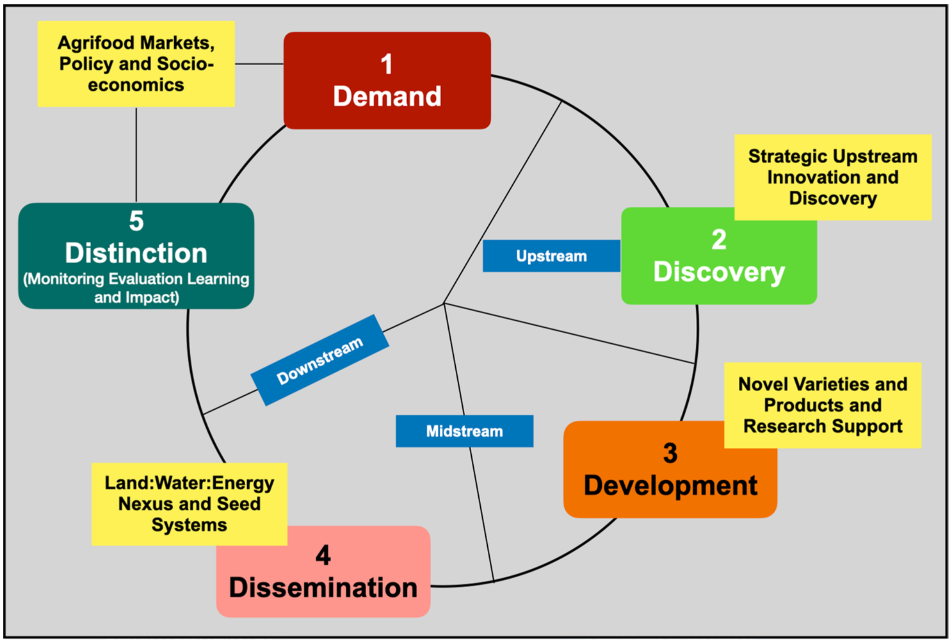

Fig. 3 The '5D' Cycle showing that a circular model consisting of demand, discovery, development, dissemination and distinction is essential to ensure that research efforts facilitate developmental goals

different stages of delivery. Thus, a circular research model (Fig. 3) that considers the monitoring, evaluation and learning to analyze if the demand has been met and it has made a socio-economic difference, should become an essential part of 'research for development'. It is clear that sustained research efforts are needed to future-proof food security. The examples cited here are mainly for rice, but the approaches are also applicable to other cereal crops.

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Declarations

Conflict of interest The authors declare that there are no competing interests.

References

3,000 rice genomes project (2014) The 3,000 rice genomes project. Gigascience. https://doi.org/10.1186/2047-217X-3-7

Achard P, Cheng H, Grauwe LD et al (2006) Integration of plant responses to environmentally activated phytohormonal signals. Science 311:91–94

Achard P, Gong F, Cheminant S, Alioua M, Hedden P, Genschik P (2008) The cold-inducible CBF1 factor–dependent signaling pathway modulates the accumulation of the growth-repressing DELLA proteins via its effect on gibberellin metabolism. Plant Cell 20:2117–2129

Ahmed F, Rafii MY, Ismail MR, Juraimi AS, Rahim HA, Asfaliza R, Latif MA (2013) Waterlogging tolerance of crops: breeding, mechanism of tolerance, molecular approaches, and future prospects. Biomed Res Int. https://doi.org/10.1155/2013/963525

Alexandratos N, Bruinsma J (2012) World agriculture towards 2030/2050: the 2012 revision. ESA Working paper No. 12-03. Rome, FAO

Allen JM, Sander BO (2019) The diverse benefits of alternate wetting and drying (AWD). Los Baños, Philippines: International Rice Research Institute (IRRI). https://hdl.handle.net/10568/101399

Ashikari M, Sasaki A, Ueguchi-Tanaka M et al (2002) Loss-of-function of a rice gibberellin biosynthetic gene, *GA20 Oxidase* (*GA20ox-2*), led to the rice 'Green Revolution.' Breed Sci 52:143–150

Bailey-Serres J, Fukao T, Ronald P, Ismail A, Heuer S, Mackill D (2010) Submergence tolerant rice: SUB1's journey from landrace to modern cultivar. Rice 3:138–147

Bailey-Serres J, Parker JE, Ainsworth EA, Oldroyd GED, Schroeder JI (2019) Genetic strategies for improving crop yields. Nature 575:109–118

Bengyella L, Hetsa BA, Fonmboh DJ, Jose RC (2020) Assessment of damage caused by evolved fall armyworm on native and transgenic maize in South Africa. Phytoparasitica. https://doi.org/10.1007/s12600-020-00862-z

Biswal AK, Shamim M, Cruzado K, Soriano G, Ghatak A, Toleco MR, Vikram P (2017) Role of biotechnology in rice production. In: Chauhan B, Jabran K, Mahajan G (eds) Rice production worldwide. Springer, Cham, pp 487–547

Brennan JP, Malabayabas A (2011) International Rice Research Institute's contribution to rice varietal yield improvement in South-East Asia. ACIAR Impact Assessment Series Report No. 74. Australian Centre for International Agricultural Research: Canberra

Buckley CR, Caine RS, Gray JE (2020) Pores for thought: can genetic manipulation of stomatal density protect future rice yields? Front Plant Sci. https://doi.org/10.3389/fpls.2019.01783

Butardo VM Jr, Sreenivasulu N (2019) Improving head rice yield and milling quality: state-of-the-art and future prospects. Methods Mol Biol 1892:1–18

Council for Agricultural Science and Technology (CAST) (2019) Aquifer depletion and potential impacts on long-term irrigated agricultural productivity. Issue Paper 63, CAST, Ames, Iowa

Custodio MC, Cuevas RP, Ynion J, Laborte AG, Velasco ML, Demont M (2019) Rice quality: how is it defined by consumers, industry, food scientists, and geneticists? Trends Food Sci Tech 92:122–137

Dalin C, Wada Y, Kastner T, Puma MJ (2017) Groundwater depletion embedded in international food trade. Nature 543:700–704

Diedhiou CJ, Popova OV, Dietz KJ, Golldack D (2008) The SNF1-type serine-threonine protein kinase SAPK4 regulates stress-responsive gene expression in rice. BMC Plant Biol. https://doi.org/10.1186/1471-2229-8-49

Dixit S, Biswal AK, Min A et al (2015) Action of multiple intra-QTL genes concerted around a co-localized transcription factor underpins a large effect QTL. Sci Rep. https://doi.org/10.1038/srep15183

Douthwaite B, Apgar JM, Schwarz AM, Attwood S, Sellamuttu SS, Clayton T (2017) A new professionalism for agricultural research for development. Int J Agric Sustain 15:238–252

Erb TJ, Zarzycki J (2018) A short history of RubisCO: the rise and fall (?) of Nature's predominant CO2 fixing enzyme. Curr Opin Biotechnol 49:100–107

Ermakova M, Danila FR, Furbank RT, von Caemmerer S (2020) On the road to C4 rice: advances and perspectives. Plant J 101:940–950

Feng L, Han Y, Liu G, An B, Yang J, Yang G, Li Y, Zhu Y (2007) Overexpression of Sedoheptulose-1,7-Bisphosphatase enhances photosynthesis and growth under salt stress in transgenic rice plants. Funct Plant Biol 34:822–834

Fukayama H, Ueguchi C, Nishikawa K, Katoh N, Ishikawa C, Masumoto C, Hatanaka T, Misoo S (2012) Overexpression of Rubisco activase decreases the photosynthetic CO2 assimilation rate by reducing rubisco content in rice leaves. Plant Cell Physiol 53:976–986

Gregorio G (1997) Tagging salinity tolerance genes in rice using amplified fragment length poly-morphism (AFLP). University of the Philippines, Los Baños

Gummert M (2013) Improved postharvest technologies and management for reducing postharvest losses in rice. Acta Hortic 1011:63–70

Guo S, Xu Y, Liu H, Mao Z, Zhang C, Ma Y, Zhang Q, Meng Z, Chong K (2013) The interaction between OsMADS57 and OsTB1 modulates rice tillering via DWARF14. Nat Commun. https://doi.org/10.1038/ncomms2542

Guo XY, Li Y, Fan J et al (2019) Host-induced gene silencing of *MoAP1* confers broad-spectrum resistance to *Magnaporthe oryzae*. Front Plant Sci. https://doi.org/10.3389/fpls.2019.00433

Harikesh KS (2018) Effect of integrated nutrient management in rice (*Oryza sativa* L.) under SRI technique: a review. J Pharmacog Phytochem 7:2539–2544

Hellin J, Balié J, Fisher E et al (2020a) Trans-disciplinary responses to climate change: lessons from rice-based systems in Asia. Climate 8:35

Hellin J, Balié J, Fisher E, Blundo-Canto G, Meah N, Kohli A, Connor M (2020b) Sustainable agriculture for health and prosperity: stakeholders' roles, legitimacy and modus operandi. Dev Prac. https://doi.org/10.1080/09614524.2020.1798357

Hoang TML, Tran TN, Nguyen TKT, Williams B, Wurm P, Bellairs S, Mundree S (2016) Improvement of salinity stress tolerance in rice: challenges and Opportunities. Agron. https://doi.org/10.3390/agronomy6040054

Huang XZ, Zeng XF, Li JR, Zhao DG (2017) Construction and analysis of *tify1a* and *tify1b* mutants in rice (*Oryza sativa*) based on CRISPR/Cas9 technology. J Agric Biotechnol 25:1003–1012

Itoh H, Shimada A, Ueguchi-Tanaka M, Kamiya N, Hasegawa Y, Ashikari M, Matsuoka M (2005) Overexpression of a GRAS protein lacking the DELLA domain confers altered gibberellin responses in rice. Plant J 44:669–679

Iuchi S, Kobayashi M, Taji T, Naramoto M, Seki M, Kato T, Tabata S, Kakubari Y, Yamaguchi-Shinozaki K, Shinozaki K (2001) Regulation of drought tolerance by gene manipulation of 9-cis-epoxycarotenoid dioxygenase, a key enzyme in abscisic acid biosynthesis in Arabidopsis. Plant J 27:325–333

Jamaloddin M, Durga Rani CV, Swathi G et al (2020) Marker Assisted Gene Pyramiding (MAGP) for bacterial blight and blast resistance into mega rice variety "Tellahamsa." PLoS ONE. https://doi.org/10.1371/journal.pone.0234088

Jan A, Maruyama K, Todaka D, Kidokoro S, Abo M, Yoshimura E, Shinozaki K, Nakashima K, Yamaguchi-Shinozaki K (2013) OsTZF1, a CCCH-tandem zinc finger protein, confers delayed senescence and stress tolerance in rice by regulating stress-related genes. Plant Physiol 161:1202–1216

Karki S, Rizal G, Quick WP (2013) Improvement of photosynthesis in rice (*Oryza sativa* L.) by inserting the C4 pathway. Rice. https://doi.org/10.1186/1939-8433-6-28

Karmakar A, Bhattacharya S, Sengupta S, Ali N, Sarkar SN, Datta K, Datta SK (2020) RNAi-mediated silencing of *ITPK* gene reduces phytic acid content, alters transcripts of phytic acid biosynthetic genes, and modulates mineral distribution in rice seeds. Rice Sci 27:315–318

Kaur R, Bhunia RK, Rajam MV (2020) MicroRNAs as potential targets for improving rice yield via plant architecture modulation: recent studies and future perspectives. J Biosci 45:116

Khan MH, Dar ZA, Dar SA (2015) Breeding strategies for improving rice yield—a review. Agric Sci 6:467–478

Khush GS (2013) Strategies for increasing the yield potential of cereals: case of rice as an example. Plant Breed 132:433–436

Kim H, Lee K, Hwang H, Bhatnagar N, Kim DY, Yoon IS, Byun MO, Kim ST, Jung KH, Kim BG (2014) Overexpression of *PYL5* in rice enhances drought tolerance, inhibits growth, and modulates gene expression. J Exp Bot 65:453–464

Kiribuchi K, Sugimori M, Takeda M et al (2004) *RERJ1*, a jasmonic acid-responsive gene from rice, encodes a basic helix-loop-helix protein. Biochem Biophys Res Commun 17:857–863

Kohli A, Venuprasad R, Swamy BPM (2019) Interfacing conventional and modern approaches to speed up and focus plant breeding. Rural 21:9–12

Kohli A, Miro B, Balié J, d'A Hughes J (2020) Photosynthesis research: a model to bridge fundamental science, translational products, and socio-economic considerations in agriculture. J Exp Bot 71:2281–2298

Komor AC, Kim YB, Packer MS, Zuris JA, Liu DR (2016) Programmable editing of a target base in genomic DNA without double-stranded DNA cleavage. Nature 533:420–424

Kosik O, Romero MV, Bandonill EH, Abilgos-Ramos RG, Sreenivasulu N, Shewry P, Lovegrove A (2020) Diversity of content and composition of cell wall-derived dietary fibre in polished rice. J Cereal Sci. https://doi.org/10.1016/j.jcs.2020.103122

Krishnamurthy P, Vishal B, Khoo K, Rajappa S, Loh CS, Kumar PP (2019) Expression of *AoNHX1* increases salt tolerance of rice and Arabidopsis, and bHLH transcription factors regulate *AtNHX1* and *AtNHX6* in Arabidopsis. Plant Cell Rep 38:1299–1315

Krishnamurthy P, Vishal B, Ho WJ, Lok FCJ, Lee FSM, Kumar PP (2020) Regulation of a Cytochrome P450 gene *CYP94B1* by WRKY33 transcription factor controls apoplastic barrier formation in roots to confer salt tolerance. Plant Physiol 184:2199–2215

Kumar PP (2013) Regulation of biotic and abiotic stress responses by plant hormones. Plant Cell Rep 32:943

Kumar VVS, Verma RK, Yadav SK, Yadav P, Watts A, Rao MV, Chinnusamy V (2020) CRISPR-Cas9 mediated genome editing of *Drought And Salt Tolerance* (*OsDST*) gene in indica mega rice cultivar MTU1010. Physiol Mol Biol Plants 26:1099–1110

Kumar A, Raman A, Yadav S et al (2021) Genetic gain for rice yield in rainfed environments in India. Field Crops Res. https://doi.org/10.1016/j.fcr.2020.107977

Kwak KJ, Kim JY, Kim YO, Kang H (2007) Characterization of transgenic Arabidopsis plants overexpressing high mobility group B proteins under high salinity, drought or cold stress. Plant Cell Physiol 48:221–231

Lakshmanan M, Mohanty B, Lee DY (2013) Identifying essential genes/reactions of the rice photorespiration by in silico model-based analysis. Rice (n Y). https://doi.org/10.1186/1939-8433-6-20

Lau OS, Davies KA, Chang J, Adrian J, Rowe MH, Ballenger CE, Bergmann DC (2014) Direct roles of SPEECHLESS in the specification of stomatal self-renewing cells. Science 345:1605–1609

Lee JS, Sreenivasulu N, Hamilton RS, Kohli A (2019) Brown rice, a diet rich in health promoting properties. J Nutr Sci Vitaminol (tokyo) 65(Supplement):S26–S28

Lesk C, Rowhani P, Ramankutty N (2016) Influence of extreme weather disasters on global crop production. Nature 529:84–87

Li M, Li X, Zhou Z, Wu P, Fang M, Pan X, Lin Q, Luo W, Wu G, Li H (2016) Reassessment of the four yield-related genes *Gn1a*, *DEP1*, *GS3*, and *IPA1* in rice using a CRISPR/Cas9 system. Front Plant Sci. https://doi.org/10.3389/fpls.2016.00377

Li Q-F, Zhou Y, Xiong M, Ren X-Y, Han L, Wang J-D, Zhang C-Q, Fan X-L, Liu Q-Q (2020) Gibberellin recovers seed germination in rice with impaired brassinosteroid signalling. Plant Sci. https://doi.org/10.1016/j.plantsci.2020.110435

Liu T, Gu JY, Xu CJ, Gao Y, An CC (2007) Overproduction of *OsSLRL2* alters the development of transgenic Arabidopsis plants. Biochem Biophys Res Commun 13:983–989

Liu X, Zhang C, Wang X, Liu Q, Yuan D, Pan G, Sun SSM, Tu J (2016) Development of high-lysine rice via endosperm-specific expression of a foreign *LYSINE RICH PROTEIN* gene. BMC Plant Biol. https://doi.org/10.1186/s12870-016-0837-x

Llorente C, Jimenez R, Jackie BY, Fernie AR, Sreenivasulu N (2019) Rice grain quality benchmarking through profiling of volatiles and metabolites in grains using gas chromatography mass spectrometry. Methods Mol Biol 1892:187–199

Long BM, Hee WY, Sharwood RE et al (2018) Carboxysome encapsulation of the CO2-fixing enzyme Rubisco in tobacco chloroplasts. Nat Commun. https://doi.org/10.1038/s41467-018-06044-0

Lou D, Wang H, Liang G, Yu D (2017) OsSAPK2 confers abscisic acid sensitivity and tolerance to drought stress in rice. Front Plant Sci. https://doi.org/10.3389/fpls.2017.00993

Lu G, Coneva V, Casaretto JA, Ying S, Mahmood K, Liu F, Nambara E, Bi Y-M, Rothstein SJ (2015) OsPIN5b modulates rice (*Oryza sativa*) plant architecture and yield by changing auxin homeostasis, transport and distribution. Plant J 83:913–925

Ludwig Y, Slamet-Loedin IH (2019) Genetic biofortification to enrich rice and wheat grain iron: from genes to product. Front Plant Sci. https://doi.org/10.3389/fpls.2019.00833

Luo Y, Yin Z (2013) Marker-assisted breeding of Thai fragrance rice for semi-dwarf phenotype, submergence tolerance and disease resistance to rice blast and bacterial blight. Mol Breed 32:709–721

Lyman NB, Jagadish KS, Nalley LL, Dixon BL, Siebenmorgen T (2013) Neglecting rice milling yield and quality underestimates economic losses from high-temperature stress. PLoS ONE. https://doi.org/10.1371/journal.pone.0072157

Mahender A, Anandan A, Pradhan SK, Pandit E (2016) Rice grain nutritional traits and their enhancement using relevant genes and QTLs through advanced approaches. Springerplus. https://doi.org/10.1186/s40064-016-3744-6

Mallikarjuna G, Mallikarjuna K, Reddy MK, Kaul T (2011) Expression of *OsDREB2A* transcription factor confers enhanced dehydration and salt stress tolerance in rice (*Oryza sativa* L.). Biotechnol Lett 33:1689–1697

Manghwar H, Lindsey K, Zhang X, Jin S (2019) CRISPR/Cas system: recent advances and future prospects for genome editing. Trends Plant Sci 24:1102–1125

McGrath JM, Long SP (2014) Can the cyanobacterial carbon-concentrating mechanism increase photosynthesis in crop species? A theoretical analysis. Plant Physiol 164:2247–2261

Meng L, Zhao X, Ponce K, Ye G, Leung H (2016) QTL mapping for agronomic traits using multi-parent advanced generation inter-cross (MAGIC) populations derived from diverse elite indica rice lines. Field Crops Res 189:19–42

Meng X, Yu H, Zhang Y, Zhuang F, Song X, Gao S, Gao C, Li J (2017) Construction of a genome-wide mutant library in rice using CRISPR/Cas9. Mol Plant 10:1238–1241

Misra G, Badoni S, Domingo CJ, Cuevas RPO, Llorente C, Mbanjo EGN, Sreenivasulu N (2018) Deciphering the genetic architecture of cooked rice texture. Front Plant Sci. https://doi.org/10.3389/fpls.2018.01405

Miura K, Ikeda M, Matsubara A, Song XJ, Ito M, Asano K, Matsuoka M, Kitano H, Ashikari M (2010) OsSPL14 promotes panicle branching and higher grain productivity in rice. Nat Genet 42:545–549

Mopera LE (2016) Food loss in the food chain: the Philippine agriculture scenario. J Dev Sustain Agric 11:8–16

Muralidharan K, Prasad GSV, Rao CS (1996) Breeding for rice improvement, where do we stand? Curr Sci 71:438–448

Muralidharan K, Prasad GSV, Rao CS, Siddiq EA (2019) Genetic gain for yield in rice breeding and rice production in India to meet with the demand from increased human population. Curr Sci 116:544–560

Nelson ARLE, Ravichandran K, Antony U (2019) The impact of the Green Revolution on indigenous crops of India. J Ethn Foods. https://doi.org/10.1186/s42779-019-0011-9

Nomura M, Higuchi T, Ishida Y, Ohta S, Komari T, Imaizumi N, Miyao-Tokutomi M, Matsuoka M, Tajima S (2005) Differential expression pattern of C4 bundle sheath expression genes in rice, a C3 plant. Plant Cell Physiol 46:754–761

Oliva R, Ji C, Atienza-Grande G et al (2019) Broad-spectrum resistance to bacterial blight in rice using genome editing. Nature Biotechnol 37:1344–1350

Pasion EA, Badoni S, Misra G, Anacleto R, Parween S, Kohli A, Sreenivasulu N (2021) OsTPR boosts the superior grains through increase in upper secondary rachis branches without incurring a grain quality penalty. Plant Biotechnol J. https://doi.org/10.1111/pbi.13560

Peleg Z, Reguera M, Tumimbang E, Walia H, Blumwald E (2011) Cytokinin-mediated source/sink modifications improve drought tolerance and increase grain yield in rice under water-stress. Plant Biotechnol 9:747–758

Peng S, Khush GS, Virk P, Tang Q, Zou Y (2008) Progress in ideotype breeding to increase rice yield potential. Field Crops Res 108:32–38

Phalan B, Green RE, Dicks LV, Dotta G, Feniuk C, Lamb A, Strassburg BBN, Williams DR, Zu Ermgassen EKHJ, Blamford A (2016) How can higher-yield farming help to spare nature? Science 351:450–451

Pingali PL (2012) Green revolution: impacts, limits, and the path ahead. Proc Natl Acad Sci USA 109:12302–12308

Platten JD, Cobb JN, Zantua RE (2019) Criteria for evaluating molecular markers: comprehensive quality metrics to improve marker-assisted selection. PLoS ONE. https://doi.org/10.1371/journal.pone.0210529

Price GD, Badger MR, von Caemmerer S (2011) The prospect of using cyanobacterial bicarbonate transporters to improve leaf photosynthesis in C3 crop plants. Plant Physiol 155:20–26

Rahman L, Khanam MS, Koh H-J (2008) QTL analysis for yield related traits using populations derived from an indica-japonica hybrid in rice (*Oryza sativa* L.). Czech J Genet Plant Breed 44:93–104

Ramamoorthy R, Vishal B, Ramachandran S, Kumar PP (2018) The *OsPS1-F* gene regulates growth and development in rice by modulating photosynthetic electron transport rate. Plant Cell Rep 37:377–385

Raorane ML, Pabuayon IM, Miro B, Kalladan R, Reza-Hajirezai M, Oane RH, Kumar A, Sreenivasulu N, Heny A, Kohli A (2015a) Variation in primary metabolites in parental and near-isogenic lines of the QTL *qDTY 12.1*: altered roots and flag leaves but similar spikelets of rice under drought. Mol Breed. https://doi.org/10.1007/s11032-015-0322-5

Raorane ML, Pabuayon IM, Varadarajan AR, Mutte SK, Kumar A, Treumann A, Kohli A (2015b) Proteomic insights into the role of the large-effect QTL *qDTY 12.1* for rice yield under drought. Mol Breed. https://doi.org/10.1007/s11032-015-0321-6

Ray DK, Ramankutty N, Mueller ND, West PC, Foley JA (2012) Recent patterns of crop yield growth and stagnation. Nat Commun. https://doi.org/10.1038/ncomms2296

Santos MV, Cuevas RPO, Sreenivasulu N, Molina L (2019) Measurement of rice grain dimensions and chalkiness, and rice grain elongation using image analysis. In: Rice Grain Quality. Humana Press, New York, pp 99-108

Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A (2019) The global burden of pathogens and pests on major food crops. Nat Ecol Evol 3:430–439

Sawada H, Shim IS, Usui K (2006) Induction of Benzoic acid 2-hydroxylase and salicylic acid biosynthesis-modulation by salt stress in rice seedlings. Plant Sci 171:263–270

Sawicka B (2019) Post-harvest losses of agricultural produce. Sustain Dev 1:1–16

Schuler ML, Mantegazza O, Weber APM (2016) Engineering C4 photosynthesis into C3 chassis in the synthetic biology age. Plant J 87:51–65

Segami S, Yamamoto T, Oki K et al (2016) Detection of novel QTLs regulating grain size in extra-large grain rice (*Oryza sativa* L.) lines. Rice. https://doi.org/10.1186/s12284-016-0109-2

Shahbandeh M (2019) Principal rice exporting countries worldwide 2018/2019. https://www.statista.com/statistics/255947/top-rice-exporting-countries-worldwide-2011

Sharma TR, Rai AK, Gupta SK, Vijayan J, Devanna BN, Ray S (2012) Rice blast management through host-plant resistance: retrospect and prospects. Agric Res 1:37–52

Shen BR, Wang LM, Lin XL et al (2019) Engineering a new chloroplastic photorespiratory bypass to increase photosynthetic efficiency and productivity in rice. Mol Plant 12:199–214

Shi CL, Dong NQ, Guo T, Ye WW, Shan JX, Lin HX (2020) A quantitative trait locus *GW6* controls rice grain size and yield through the gibberellin pathway. Plant J 103:1174–1188

Singh VK, Singh A, Singh SP et al (2013) Marker-assisted simultaneous but stepwise backcross breeding for pyramiding blast resistance genes *Piz5* and *Pi54* into an elite Basmati rice restorer line 'PRR78.' Plant Breed 132:486–496

Song Y, Wang L, Xiong L (2009) Comprehensive expression profiling analysis of *OsIAA* gene family in developmental processes and in response to phytohormone and stress treatments. Planta 229:577–591

Sparks A, Nelson A, Castilla N (2012) Where rice pests and diseases do the most damage. Rice Today 11:27

Spindel J, Begum H, Akdemir D, Virk P, Collard B, Redona E, Atlin G, Jannink JL, McCouch SR (2015) Genomic selection and association mapping in rice (*Oryza sativa*): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding lines. PLoS Genet. https://doi.org/10.1371/journal.pgen.1004982

Sravan US, Murthy KVR (2014) Scope of pre-kharif crops for productivity enhancement of rice based cropping system in north coastal zone of Andhra Pradesh. Res J Agric Sci 5:1100–1103

Sravan US, Murthy KVR (2018) Enhancing productivity in rice-based cropping systems, plant competition in cropping systems Daniel Dunea. IntechOpen,. https://doi.org/10.5772/intechopen.76904

Sun YW, Jiao GA, Liu ZP et al (2017) Generation of high-amylose rice through CRISPR/Cas9-Mediated targeted mutagenesis of starch branching enzymes. Front Plant Sci. https://doi.org/10.3389/fpls.2017.00298

Suzuki Y, Kondo E, Makino A (2017) Effects of co-overexpression of the genes of Rubisco and transketolase on photosynthesis in rice. Photosynth Res 131:281–289

Swamy BPM, Rahman MA, Inabangan-Asilo MA, Amparado A, Manito C, Chadha-Mohanty P, Reinke R, Slamet-Loedin IH (2016) Advances in breeding for high grain zinc in rice. Rice. https://doi.org/10.1186/s12284-016-0122-5

Swamy BPM, Descalsota GIL, Nha CT, Amparado A, Inabangan-Asilo MA, Manito C, Tesoro F, Reinke R (2018) Identification of genomic regions associated with agronomic and biofortification traits in DH populations of rice. PLoS ONE. https://doi.org/10.1371/journal.pone.0201756

Swamy BPM, Samia M, Boncodin R et al (2019) Compositional analysis of genetically engineered GR2E "Golden Rice" in comparison to that of conventional rice. J Agric Food Chem 67:7986–7994

Trijatmiko KR, Duenas C, Tsakirpaloglou N et al (2016) Biofortified indica rice attains iron and zinc nutrition dietary targets in the field. Sci Rep. https://doi.org/10.1038/srep19792

Tripathi AD, Mishra R, Maurya KK, Singh RB, Wilson DW (2019) Estimates for world population and global food availability for global health role. Funct Food Security Glob Health. https://doi.org/10.1016/b978-0-12-813148-0.00001-3

Tu J, Zhang G, Datta K, Xu C, He Y, Zhang Q, Khush GS, Datta SK (2000) Field performance of transgenic elite commercial hybrid rice expressing *Bacillus thuringiensis* delta-endotoxin. Nature Biotechnol 18:1101–1104

Verma V, Ravindran P, Kumar PP (2016) Plant hormone-mediated regulation of stress responses. BMC Plant Biol. https://doi.org/10.1186/s12870-016-0771-y

Vikram P, Swamy BP, Dixit S, Singh R, Singh BP, Miro B, Kohli A, Henry A, Singh NK, Kumar A (2015) Drought susceptibility of modern rice varieties: an effect of linkage of drought tolerance with undesirable traits. Sci Rep. https://doi.org/10.1038/srep14799

Vishal B, Krishnamurthy P, Ramamoorthy R, Kumar PP (2019) OsTPS8 controls yield-related traits and confers salt stress tolerance in rice by enhancing suberin deposition. New Phytol 221:1369–1386

Walker BJ, South PF, Ort DR (2016a) Physiological evidence for plasticity in glycolate/glycerate transport during photorespiration. Photosynth Res 129:93–103

Walker BJ, VanLoocke A, Bernacchi CJ, Ort DR (2016b) The costs of photorespiration to food production now and in the future. Annu Rev Plant Biol 67:107–129

Wang C, Yang Y, Wang H, Ran X, Li B, Zhang J, Zhang H (2016) Ectopic expression of a cytochrome P450 monooxygenase gene *PtCYP714A3* from *Populus trichocarpa* reduces shoot growth and improves tolerance to salt stress in transgenic rice. Plant Biotechnol J 14:1838–1851

Wang W, Mauleon R, Hu Z et al (2018) Genomic variation in 3,010 diverse accessions of Asian cultivated rice. Nature 557:43–49

Werner T, Nehnevajova E, Köllmer I, Novákb O, Strnadb M, Krämerc U, Schmülling T (2010) Root-specific reduction of cytokinin causes enhanced root growth, drought tolerance, and leaf mineral enrichment in Arabidopsis and Tobacco. Plant Cell 22:3905–3920

Wu Q, Zhang W, Pwee KH, Kumar PP (2003a) Cloning and characterization of rice *HMGB1* gene. Gene 312:103–109

Wu Q, Zhang W, Pwee KH, Kumar PP (2003b) Rice HMGB1 protein recognizes DNA structures and bends DNA efficiently. Arch Biochem Biophys 411:105–111

Xu R, Yang Y, Qin R, Li H, Qiu C, Li L, Wei P, Yang J (2016) Rapid improvement of grain weight via highly efficient CRISPR/Cas9-mediated multiplex genome editing in rice. J Genet Genomics 43:529–532

Yamori W, Masumoto C, Fukayama H, Makino A (2012) Rubisco activase is a key regulator of non-steady-state photosynthesis at any leaf temperature and to a lesser extent, of steady-state photosynthesis at high temperature. Plant J 71:871–880

You J, Zong W, Hu H, Li X, Xiao J, Xiong L (2014) A stress-responsive NAC1-regulated protein phosphatase gene *Rice Protein Phosphatase 18* modulates drought and oxidative stress tolerance through abscisic acid-independent reactive oxygen species scavenging in rice. Plant Physiol 166:2100–2114

Yuan L (2017) Progress in super-hybrid rice breeding. Crop J 5:100–102

Zeng Y, Wen J, Zhao W, Wang Q, Huang W (2020) Rational improvement of rice yield and cold tolerance by editing the three genes *OsPIN5b*, *GS3*, and *OsMYB30* with the CRISPR–Cas9 system. Front Plant Sci. https://doi.org/10.3389/fpls.2019.01663

Zetsche B, Gootenberg JS, Abudayyeh OO et al (2015) Cpf1 is a single RNA-guided endonuclease of a class 2 CRISPR-Cas system. Cell 163:759–771

Zhang Z, Li F, Li D, Zhang H, Huang R (2010) Expression of ethylene response factor *JERF1* in rice improves tolerance to drought. Planta 232:765–774

Zhang Q, Li J, Zhang W et al (2012) The putative auxin efflux carrier OsPIN3t is involved in the drought stress response and drought tolerance. Plant J 72:805–816

Zhang A, Liu Y, Wang F et al (2019) Enhanced rice salinity tolerance via CRISPR/Cas9-targeted mutagenesis of the *OsRR22* gene. Mol Breed. https://doi.org/10.1007/s11032-019-0954-y

Zulfugarov IS, Tovuu A, Eu YJ et al (2014) Production of superoxide from Photosystem II in a rice (*Oryza sativa* L.) mutant lacking PsbS. BMC Plant Biol. https://doi.org/10.1186/s12870-014-0242-2