Engineering rice genomes towards green super rice
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Rice, cultivated for millennia across diverse geographical regions, has witnessed tremendous advancements in recent decades, epitomized by the emergence of Green Super Rice. These efforts aim to address challenges such as climate change, pest and disease threats, and sustainable agriculture. Driven by the advent of multiomics big data, breakthroughs in genomic tools and resources, hybrid rice breeding techniques, and the extensive utilization of green genes, rice genomes are undergoing delicate modifications to produce varieties with high yield, superior quality, enhanced nutrient efficiency, and resilience to pests and environmental stresses, leading to the development of green agriculture in China. Additionally, the utilization of wild relatives and the promotion of genomic breeding approaches have further enriched our understanding of rice improvement. In the future, international efforts to develop next-generation green rice varieties remain both challenging and imperative for the whole community.

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Introduction
Rice has been a fundamental staple crop for millennia supporting more than half of the world's population and serving as a cornerstone of food security across diverse geographical regions. The history of rice cultivation highlights its pivotal role in human civilization, from ancient agricultural practices to modern farming technique [1]. As the growing number of global populations, the importance of rice in food security continue to increase. However, the cultivation of rice faces numerous challenges, including overuse of nitrogenous fertilizers for yielding [2], the impacts of climate change [3], increasing pest and disease threats [4], and the pressing need for sustainable agricultural practices [5].

In recent decades, significant advancements have been made in rice genetics and breeding to address these challenges, epitomized by the emergence of Green Super Rice (GSR). This initiative aims to develop rice varieties that are not only high-yielding and of superior quality but also resilient to environmental stresses and efficient in nutrient use [6]. GSR represents a comprehensive approach to sustainable agriculture, incorporating multiomics big data, breakthroughs in genomic tools, hybrid rice breeding techniques, and the extensive utilization of green genes. These efforts are crucial in mitigating the adverse effects of climate change on rice cultivation, combating pests and diseases, and promoting sustainable farming practices, thereby ensuring the continued global significance of rice as a staple crop.

Multiomics big data driving GSR
The advent of big data from various omics technologies – genomics, transcriptomics, proteomics, and metabolomics – has revolutionized the field of crop improvement, particularly in the GSR development. Genomics lays the foundation of multiomics data, which starts since the release of the reference genome of a *japonica* variety Nipponbare [7,8]. An increasing number of high-quality rice genomes, even the cracking of gap-free reference genomes, have been achieved through community efforts [9—13]. Modern high-throughput sequencing technologies further generate vast amounts of genomic data, revealing genetic diversity within rice populations and enabling the discovery of more presence-absence variants at the pan-genome level [14—16]. The consequent genome databases and proposed strategies (Table 1) have further empowered breeders to employ techniques like marker-assisted selection and genomic selection, thereby accelerating the development of GSR varieties.

Transcriptomics offers insights into gene expression patterns under various conditions, from the dynamic expression atlas covering entire rice life cycle [17] to transcriptome analyses at the population level [18,19]. In addition, transcriptomic analyses can reveal how rice plants respond to environment at the molecular level, guiding the development of GSR varieties that can
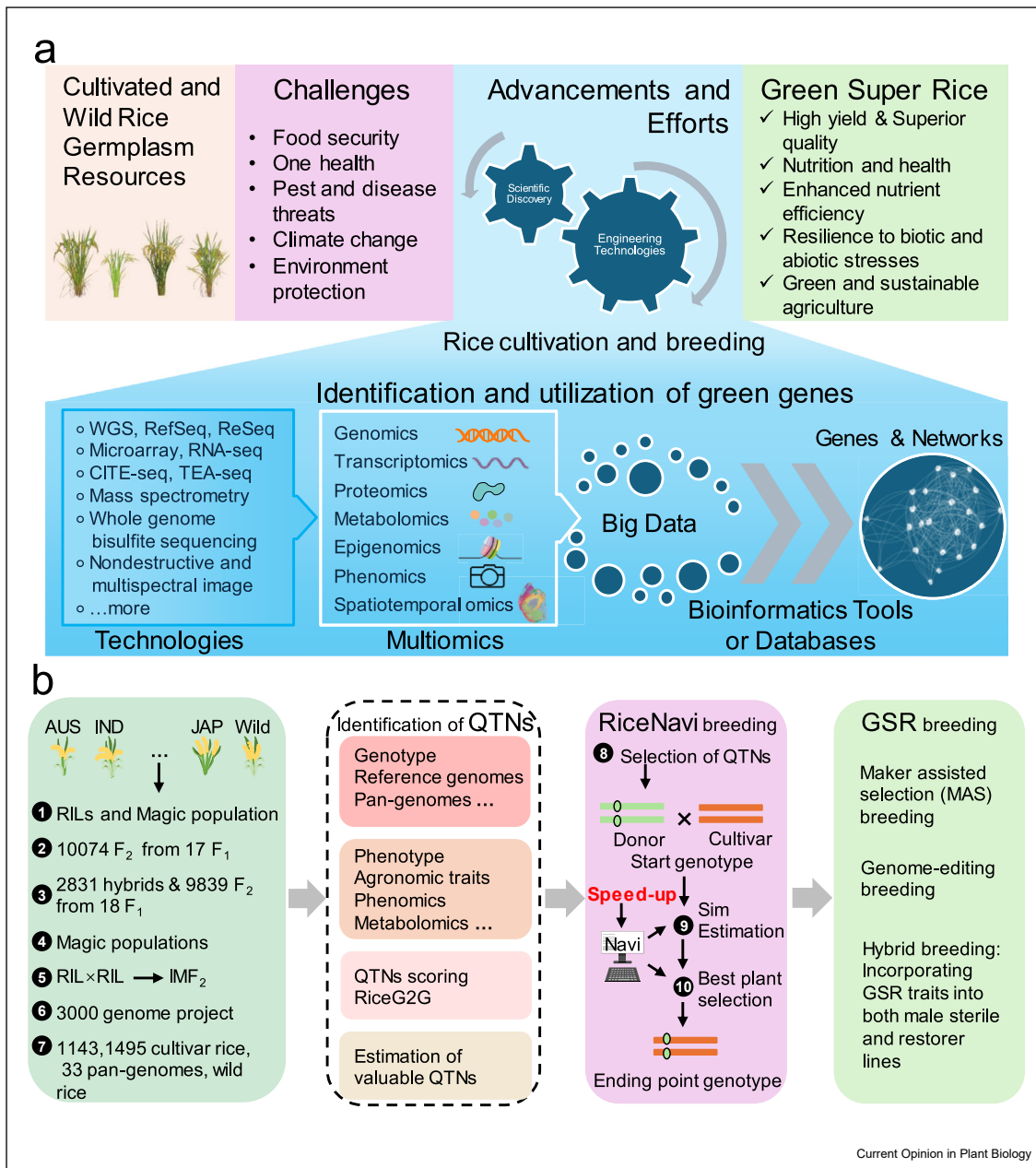
Table 1

Online databases and bioinformatics tools for rice research.

Type	Name	Description	URL[a]	Reference
Genomics	Gramene Oryza	Comparative plant genomics focused on rice varieties	https://oryza.gramene.org/	Tello-Ruiz et al., 2022. *In Plant bioinformatics: methods and protocols*, pp. 101-131
	OryGenesDB	A database for rice reverse genetics	https://orygenesdb.cirad.fr/	Droc G et al., 2006. *Nucleic Acids Res*, 34: D736-D740
	Oryzabase	An integrated biological and genome information database for rice	https://shigen.nig.ac.jp/rice/oryzabase/	Kurata and Yamazaki. 2006. *Plant Physiol*, 140: 12-17
	OryzaGenome	Genome diversity database of 21 wild *Oryza* species	http://viewer.shigen.info/oryzagenome2detail/index.xhtm	Ohyanagi et al., 2016. *Plant Cell Physiol*, 57: e1
	RAP-DB	An integrative and interactive database for rice genomics based on the *Oryza sativa* ssp. *japonica* cv. Nipponbare genome IRGSP-1.0.	https://rapdb.dna.affrc.go.jp/	Sakai et al., 2013. *Plant Cell Physiol*, 54: e6
	RGAP	Sequence and annotation data for the genome IRGSP-1.0 by the rice genome annotation project	https://rice.uga.edu/	Kawahara et al., 2013. *Rice*, 6: 4
	Rice diversity	A collaborative effort to explore the genetic basis of variation in rice and its wild ancestors	https://www.ricediversity.org/	NA
	Rice gene index	RGI: An ortholog-based pan-genome database for comparative and functional genomics of asian rice	https://riceome.hzau.edu.cn/	Yu et al., 2023. *Mol Plant*, 16: 798-801
	Rice RC	A web-based tool for browsing a set of genome assemblies, annotations, structural variations	https://ricerc.sicau.edu.cn/	Qin et al., 2021. *Cell*, 184: 3542-3558
	RiceRelativesGD	A genomic database of rice relatives by providing gene and genomic resources of 14 rice relatives from poaceae	http://ibi.zju.edu.cn/ricerelativesgd/	Mao et al., 2019. *Database*, 2019: baz110
	RIGW	A bioinformatics platform for two elite *indica* rice genomes	https://rice.hzau.edu.cn/rice_rs3/	Song et al., 2018. *Mol Plant*, 11: 505-507
	RPAN	A pan-genome browser of sequences, annotations, presence-absence variations, and gene expression profiles for 3010 rice accessions	https://cgm.sjtu.edu.cn/3kricedb/	Sun et al., 2017. *Nucleic Acids Res*, 45: 597-605
Multi-omics	CREP	A dynamic gene expression atlas covering the entire life cycle of two indica rice varieties, Minghui 63 and Zhenshan 97	https://crep.ncpgr.cn/	Wang et al., 2010. *Plant J*, 61: 752-766
	CART	Chromatin accessibility of rice tissues	https://biobigdata.nju.edu.cn/cart/	Zhu et al., 2024. *Nat Commun*, 15:6562
	Ensemble plants	An integrated omics infrastructure for *Oryza* species	https://plants.ensembl.org/Oryza_sativa/Info/Index	Kersey et al., 2018. *Nucleic Acids Res*, 46: D802-D808
	Information Commons for rice	IC4R: a Curated database providing rice genome sequences, updating rice gene annotations and integrating multiple omics data through community-contributed modules	https://ngdc.cncb.ac.cn/ic4r/	Sang et al., 2020. *Genomics, Proteomics & Bioinformatics*, 18: 161-172
	Plant reactome	Plant pathway exploration and OMICS data analysis	https://plantreactome.gramene.org	Gupta et al., 2024. *Nucleic Acids Res*, 52: D1538-D1547
	RECoN	Rice environment coexpression network for systems level analysis of abiotic-stress response	https://plantstress-pereira.uark.edu/RECoN/	Krishnan et al., 2017. *Front Plant Sci*, 8: 1640
	Rice expression database	RED: An integrated RNA-Seq-derived gene expression database for rice	https://ngdc.cncb.ac.cn/red/index	Xia et al., 2017. *J Genet Genomics*, 44: 235-241

	Rice SNP-seek database	Genotype, phenotype, and variety information of 3000 rice varieties	https://snpseek.irri.org/index.zul	Alexandrov et al., 2015. *Nucleic Acids Res*, 43: D1023-D1027; Mansueto et al., 2017. *Nucleic Acids Res*, 45: D1075-D1081
	RiceFREND	A gene coexpression database in rice based on a large collection of microarray data derived from various tissues/organs at different stages of growth and development under various conditions	https://ricefrend.dna.affrc.go.jp/	Sato et al., 2013. *Nucleic Acids Res*, 41: D1214-D1221
	RiceMetaSysB	A database of blast and bacterial blight responsive genes in rice	https://14.139.229.201/RiceMetaSysB/	Sureshkumar et al., 2019. *Database*, 2019: baz015
	RiceXPro	A repository of gene expression profiles derived from microarray analysis of tissues/organs encompassing the entire growth of the rice plant under various conditions	https://ricexpro.dna.affrc.go.jp/	Sato et al., 2013. *Nucleic Acids Res*, 41: D1206-D1213
	Transcriptome ENcyclopedia of rice	TENOR: a Database encompassing large-scale mRNA sequencing data obtained from rice under a wide variety of conditions	https://tenor.dna.affrc.go.jp/	Kawahara et al., 2016. *Plant Cell Physiol*, 57: e7
QTNs scoring	RiceNavi	A molecular breeding optimization tool based on a comprehensive map of rice quantitative trait nucleotides	http://www.xhhuanglab.cn/tool/RiceNavi.html	Wei et al., 2021. *Nat Genet*, 53: 243-253
Estimation of QTNs	RiceVarMap	A comprehensive database for rice genomic variation and its functional annotation by providing curated information from sequencing data of 4726 rice accessions	https://ricevarmap.ncpgr.cn/	Zhao et al., 2015. *Nucleic Acids Res*, 43: D1018-D1022; Zhao et al., 2021. *Mol Plant*, 14: 1584-1599
	MBKbase	An integrated omics knowledgebase for molecular breeding in rice	https://www.mbkbase.org/rice	Peng et al., 2020. *Nucleic Acids Res*, 48: D1085-D1092
Others	China rice data Center	Collective data information of rice germplasm, varieties, mutants, molecular markers, genes & QTLs, etc.	https://www.ricedata.cn/index.htm	NA
	funRiceGenes	A dataset for comprehensive understanding and application of rice functional genes	https://funricegenes.github.io/	Yao et al., 2018. *Gigascience*, 7:gix119
	Rice Tos17 insertion Mutant database	A database of rice mutant lines induced by rice retrotransposon *Tos17*	https://tos.nias.affrc.go.jp/	Miyao et al., 2003. *The Plant Cell*, 15: 1771-1780
	RiceENCODE	A comprehensive rice encyclopedia of DNA elements database for rice epigenomics	https://glab.hzau.edu.cn/RiceENCODE/	Xie et al., 2021. *Mol Plant*, 14: 1604-1606
	RiceNet	An improved network prioritization server for rice genes	https://www.inetbio.org/ricenet/	Lee et al., 2015. *Nucleic Acids Res*, 43: W122–W127
	RiceSuperPIRdb	An interactive web-based browser for the pan-genome of wild & cultivated rice project	https://www.ricesuperpir.com/	Shang et al., 2022. *Cell Res*, 32: 878-896
	RiTE-db	Collection of repeated sequences and transposable elements of several species of the *Oryza* genus, and the closely-related *Leersia perrieri*	https://omap.org/cgi-bin/rite/index.cgi	Copetti et al., 2015. *BMC Genomics*, 16: 538
	Thai rice starch database	ThRSDB: a Large collection of data on Thai rice starch composition, molecular structure, and functionality for research and industrial uses.	https://thairicestarch.kku.ac.th/en/index.html	Wanichthanarak and thitisaksakul. 2020. *Database*, 2020: baaa068

[a] The URLs were updated and accessible as of October 11th, 2024.

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Figure 1

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Progression of rice cultivation towards Green Super Rice.
(a) An overview of the development of Green Super Rice. This diagram illustrates the evolution from traditional rice cultivation to the development of Green Super Rice, highlighting key challenges, advancements, and future efforts required for sustainable and resilient rice production. It encompasses the identification and utilization of green genes for rice cultivation and breeding through the integration of various engineering technologies and scientific discoveries. Advancements in genomics, transcriptomics, proteomics, metabolomics, and other omics technologies, alongside the application of multiomics big data and bioinformatics tools and databases, are pivotal in producing rice varieties with high yield, superior quality, enhanced nutrient efficiency, and resilience to biotic and abiotic stresses. The ultimate goal is to achieve green and sustainable agriculture, addressing challenges such as food security, pest and disease threats, climate change, and environmental protection. **(b) Strategies for high-efficiency breeding schemes driven by multiomics and new technologies.** Different rice genetic populations are designed for genomic variation analysis, mapping, and gene cloning, including ① a set of more than 18,000 rice lines derived from 16 parental accessions of diverse geographic origins (Wei et al., 2024. *Science*, 385: eadm8762); ② an F_2 population from 17 representative hybrid rice crosses (Huang et al., 2016. *Nature*, 537: 629−633), ③ 2839 hybrid rice cultivars and 9839 F_2 individuals derived from 18 elite hybrid crosses (Gu et al., 2023. *Nat Genet*, 55: 1745−1756); ④ a multiparent advanced generation intercross (MAGIC) population developed from 8 varieties representing five subgroups of rice (Wang et al., 2024. *Natl Sci Rev*, 11: nwae222); ⑤ an "immortalized F_2" population generated by intermating the RILs derived from elite hybrid SY63 (Hua et al., 2002. *Genetics*, 162: 1885−1895); ⑥ genome sequences of 3010 diverse Asian cultivated rice lines (Wang et al., 2018. *Nature*, 557: 43−49); ⑦ genome sequences of 1143 *indica* rice varieties mostly selected from the parents of superior hybrid rice cultivars in China (Lv et al., 2020. *Nat Commun*, 557: 11: 4778), genome sequences of 1495 elite hybrid rice and their

thrive under such adverse conditions [20]. Complementing this, proteomics, the large-scale study of proteins, provides a direct measure of the functional molecules within cells [21,22]. Furthermore, metabolomics focuses on the comprehensive profiling of metabolites, the small molecules involved in metabolism, providing a snapshot of the physiological state of a plant and indicating how plants respond to environment [23,24]. Certainly, with the emerging of new omics such as translatomics [25], three-dimensional genomics [26], epigenomics [27] and phenomics [28], researchers have gained a holistic view of rice growth and environmental responses, enabling identification of key regulatory networks, pathways and biomarkers associated with desirable traits at different levels, facilitating the selection and breeding of GSR varieties.

Hence, in practical terms, multiomics big data has driven the development of more databases and bioinformatics tools that support GSR breeding programs. These resources provide breeders with access to vast datasets and analytical tools for identifying candidate genes, understanding their functions, and predicting the outcomes of genetic modifications (Figure 1a). As a result, the breeding cycle is significantly shortened, and the precision of developing high-performing GSR varieties is greatly increased using breeding strategies such as RiceG2G and RiceNavi (Figure 1b) [29,30]. In future, multi-omics research at single-cell resolution with spatial and developmental trajectories [31] would further provide a systems-level understanding of rice biology, facilitating precision agriculture under climate challenges.

Green genes identified in the rice genome

Following an international coordinated effort, by June 13th, 2024, a reservoir of 4567 rice genes was functionally characterized (https://funricegenes.github.io/). The genes responsible for agronomically desirable phenotypes are of special interest to the rice community, especially for those desired for resource-saving and environmentally friendly crop production [1,6]. With the aim of sustainable agriculture, green genes ensuring resistance to major diseases and insects, high efficiency in nutrient utilization, resistance to drought, salinity, flooding and other abiotic stresses, and high yield with good quality greatly promote the breeding of GSR.

Rice diseases and insect pests are the most devastating disasters in production, with the most severe cases potentially causing up to 50%−75 % yield losses [32]. Fungal blast and bacterial blight are two major diseases affecting rice production worldwide. To date, a total of 42 resistance (*R*) genes have been cloned for rice blast; with the exception of four genes, *Pi-d2*, *pi21*, *Bsr-d1* and *Ptr*, all the other genes encode nucleotide-binding site and leucine-rich repeat domain (NBS-LRR) proteins [33−36]. For bacterial blight, *Xa1* encodes an NBS-LRR protein, and the other ten cloned genes encode receptor-like kinase (RLK) (*Xa21*, *Xa3*/*Xa26* and *Xa4*), sugar will eventually be exported transporter (SWEET) (*xa13*, *xa25* and *xa41*), executor genes (*Xa10*, *Xa23* and *Xa27*) and other types (*xa5*) [37]. The brown planthopper (BPH) is the most significant pest causing rice yield reduction. Fifteen genes for BPH resistance have been isolated; *Bph14* was the first cloned gene [38], and *Bph1/9*, *Bph2*, *Bph3*, *Bph4* and *Bph6*, have been widely used in breeding [39,40]. Interestingly, nine BPH genes are NBS-LRR proteins, highlighting the similarities between insect and disease resistance.

Drought stress, floods, temperature and salinity are increasing threats to rice production. Due to the complexity of drought resistance, only a few genes, such as *DRO1*, *SNAC1* and *DRG9*, have been cloned [41−43]. *SUB1* enhances waterlogging tolerance by disrupting the typical elongation escape strategy of rice [44]. Among the temperature stress genes, *TT1*, *TT2*, *TT3.1*, *TT3.2*, *SLG1*, *AET1*, *CATB*, and *OsHTAS* confer high-temperature tolerance at various developmental stages [34,45]. *COLD1*, and *HAN1* are involved in rice cold resistance [46,47]. In addition, *SKC1* and *AT1/GS3* play major roles in salt and alkaline tolerance [48,49]. Apparently, rice adaptation to abiotic stress involves a wide range of pathways and functional genes, from specific stress signalling receptors to signal transduction components.

A lower nutrient use efficiency in rice production leads to higher investment costs, increased atmospheric greenhouse gas emissions, groundwater pollution, and surface water eutrophication. To date, a number of potentially useful nitrogen use efficiency (NUE) genes, such as *OsGATA8*, *OsTCP19*, *NGR5*, *GRF4*, *OsNR2*, *OsNRT1.1B*, *Ghd7* and *DEP1*, have been identified in crop plants [34,50]. These genes coordinate yield and NUE by participating in nitrate absorption and transport, tillering, and the gibberellic acid signalling pathway. Genes such as *PSTOL1* and *OsPHO1;2* play crucial roles in the efficient use of phosphorus.

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inbred parental lines (Huang et al., 2015. *Nat Commun*, 6: 6258: 4778), pan-genome analysis of 33 genetically diverse rice varieties (Qin et al., 2021. *Cell*, 184: 3542−3558) and the genome sequences of 446 wild rice species, *Oryza rufipogon* (Huang et al., 2012. *Nature*, 490: 497−501). Quantitative trait nucleotides (QTNs) are identified using high-quality genotypes and multiple phenotypes, including agronomic traits and multiomics traits. Rice GWAS to Gene (RiceG2G) refers to an integrated genomics approach designed to systematically prioritize causal genes and variants at trait-associated loci. It can be used to incorporate multi-omics data to further narrow down the candidate range and identify the most likely causal QTN. The valuable QTN haplotypes are estimated on the basis of genetic variation. The rice genome navigation (RiceNavi) system, which pyramids the QTN and optimizes the breeding route by simulating various scenarios for in silico breeding, was subsequently developed for rapid and precise breeding of cultivar rice and GSR. RiceNavi includes RiceNavi-QTNpick ⑧, -SimEstimation ⑨ and -SampleSelect ⑩ modules. Additionally, the application of genome-editing breeding, marker-assisted selection (MAS) breeding and hybrid breeding strategies would accelerate the breeding process of GSR.

Figure 2
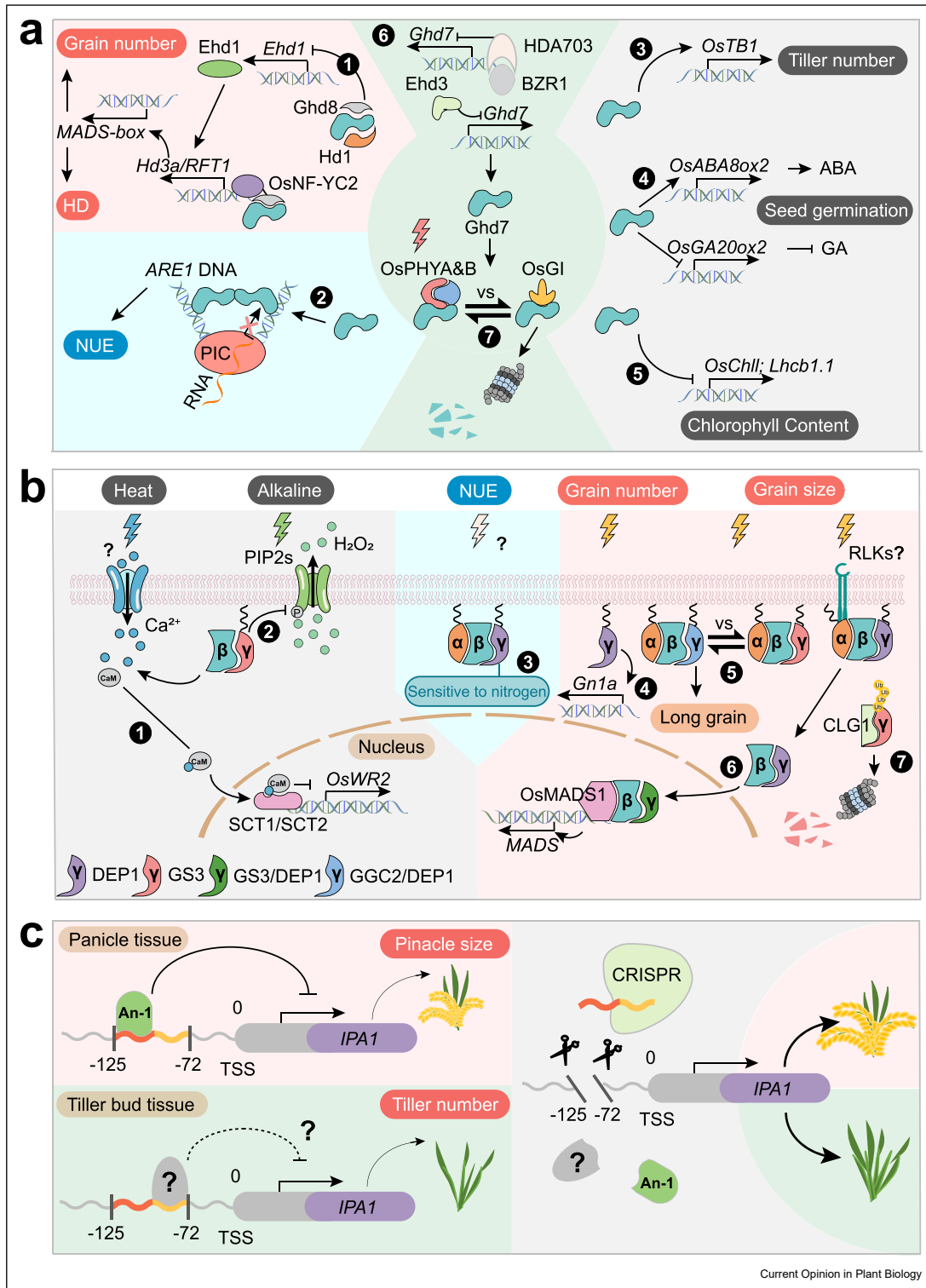
Representative cases of rice genes with pleiotropic effects.
(a) Ghd7 plays pleiotropic roles in grain number, heading date, NUE, tiller number, seed germination, and chlorophyll content. (1) Ghd7 and Ghd8 can interact with Hd1 and form a ternary repressive complex to mediate End1 (Cai et al., 2019. *Plant Cell Rep*, 38: 521–532). End1 promotes the expression of the florigen genes *Hd3a* and *RFT1* and thus induces the expression of MADS-box transcription factor family genes that control grain number and heading date (Taoka et al., 2011. *Nature*, 476: 332-U397). Ghd7, Ghd8 and OsNF-YC2 form a complex and exhibit robust binding activity with the Hd3a promoter region *in vitro* (Shen et al., 2020. *The Plant Cell*, 32: 3469–3484). (2) Ghd7 genetically acts upstream of *ARE1*, a negative regulator of NUE, to positively regulate nitrogen utilization (Wang et al., 2021. *Mol Plant*, 14: 1012–1023). PIC, preinitiation complex. (3–5) Ghd7 acts upstream of *OsTB1*, *OsABA8ox2*, *OsGA20ox2*, *OsChlI*

Grain yield is an everlasting pursuit of rice breeders. As a complex agronomic trait, the grain yield is multiplicatively determined by grains per panicle, grain weight and panicles per plant. A large number of genes that regulate the number of grains per panicle, such as *Gn1a*, *GY3*, *Ghd7*, *Ghd7.1*, *Hd1* and *Ghd8*, have been cloned [34,51]. Grain weight, which is largely influenced by grain size (length, width, and thickness), is controlled by genes such as *GS3*, *GW2*, *GS5*, *GW5*, *GW7* and *GW8* that involved in G-protein signalling, BR signalling, and SPL family transcription factor pathways [52]. Tiller number is regulated by a complex network of hormonal, genetic, and environmental factors. For example, *MOC1* controls tillering by encoding a GRAS protein that initiates axillary buds and promotes their outgrowth [53].

On this basis, grain quality is improved by dissecting genes regulating amylose content, gel consistency, gelatinization temperature and protein content. *Wx*, *ALK*, *OsbZIP58*, *OsNF-YB1*, *OsMADS29* and *Chalk5* are the main determinant genes for improving eating and cooking quality [52]. Currently, cultivating whole grain rice might represent another approach for improving quality. Compared to polished rice, whole-grain rice can retain ~80 % of the additional nutrients and beneficial components in the bran, with an increase of 30 % in the edible portion. Therefore, promoting whole-grain rice production could promote both grain yield and quality and is crucial for enhancing human nutrition.

Filling the gaps from green genes to green traits

Optimizing the pleiotropic effect of green genes

Currently, we have a handful of genes targeting "green" traits, but stacking multiple useful genes may not actually create an ideal variety, most likely due to pleiotropy, linkage drags, and complex interactions between genes and the environment. Genes with pleiotropic effects may act as transcription factors targeting multiple genes. For example, *Ghd7* regulates NUE, seed dormancy, chlorophyll content, vascular bundle variations, stress response, flowering time and grain number by regulating downstream gene expression (Figure 2a). Gγ proteins *GS3* and *DEP1* also affect diverse biological processes including grain size and weight, panicle architecture and grain number, NUE, biotic resistance, and abiotic resistance (Figure 2b). Similarly, a single transcription factor, *IPA1*, affects grain size [52], immunity [54], plant architecture, tiller number and grain number [55,56]. Thus, a major challenge is to combine all of favorable alleles into a single cultivar and balance different phenotypic effects.

One possible strategy is to precisely edit the specific cis-regulatory region of a pleiotropic gene to define the expression pattern as needed. Taking *IPA1* as an example, deleting a 54-base pair cis-regulatory region in its promoter can resolve the tradeoff between grains per panicle and tiller number, leading to increased yield potential (Figure 2c). *Xa13* provides another example, as a partial sequence deletion of the promoter improved disease resistance without affecting fertility [57]. Another approach to solve pleiotropy is to optimize the phenotype by proper combination of multiple effective genes. For example, heterozygotes of *Ghd7* and *Ghd7.1* exhibited positive dominance effects on spikelets per panicle and heading date, whereas negative dominance by *Hd1* and *Hd3a/RFT1* contributed to early flowering; therefore, quadruple heterozygotes of the four loci can create an optimal phenotype with high spikelets per panicle but slightly early flowering [58].

Solving the linkage drag with an improved strategy
Linkage drags pose another challenge for the utilization of green genes. For example, *Wx* for amylose content,

and *Lhcb1.1* to regulate tiller number, seed germination, and chlorophyll content (Hu et al., 2021. *The Crop Journal*, 9: 297−304; Weng et al., 2014. *Plant Physiol*, 164: 735−747; Wang et al., 2015. *Mol Plant*, 8: 946−957). (6) HDA703 interacts with OsBZR1 and directly targets *Ghd7* to repress its expression through histone H4 deacetylation (Wang et al., 2020. *The Plant Journal*, 104: 447−459). *Ehd3* represses the expression of *Ghd7* under long-day conditions (Matsubara et al., 2011. *The Plant Journal*, 66: 603−612). (7) OsPHYA and OsPHYB directly interact with Ghd7, blocking the OsGI-mediated 26S proteasome-dependent Ghd7 degradation pathway and thereby stabilizing the Ghd7 protein (Zheng et al., 2019. *New Phytol*, 224: 306−320). **(b) The Gγ proteins GS3, DEP1, and GGC2 are involved in diverse regulatory pathways, such as heat stress, alkaline stress, NUE, grain number, and grain size.** (1) GS3 promotes calcium influx in response to heat treatment, which facilitates Ca^{2+}-CaM signalling and enhances the interaction between SCT1-CaM, thereby reducing the transcription of *OsWR2* and affecting cuticular wax and thermotolerance under heat stress (Kan et al., 2022. *Nat Plants*, 8:53−67). (2) GS3 suppresses the phosphorylation of aquaporins PIP2s, which leads to the overaccumulation of H$_2$O$_2$ and results in alkaline stress sensitivity in crops (Zhang et al., 2023. *Science*, 379: eade8416). (3) DEP1 interacts with the Gα subunit RGA1 and the Gβ subunit RGB1 to regulate NUE in rice (Liu et al., 2022. *Annu Rev Plant Biol*, 73: 523−551). (4) The truncated version of DEP1 (dep1) downregulates the expression of *Gn1a* (Huang et al., 2009. *Nat Genet*, 41: 494−497), a cytokinin oxidase/dehydrogenase that regulates meristematic activity, panicle branching and grain number through its effect on cytokinin levels (Ashikari et al., 2005. *Science*, 309: 741−745). (5) DEP1/GGC2 and GS3 regulate grain size by competitively interacting with Gβ (Sun et al., 2018. *Nat Commun*, 9: 851). (6) Receptor-like protein kinase (RLK) interacts with the Gα subunit and activates Gβγ signalling. The Gγ subunits GS3 and DEP1 interact with OsMADS1 and function as cofactors of OsMADS1, enhancing its transcriptional activity and promoting the expression of *OsMADS1* target genes to regulate grain size (Liu et al., 2018. *Nat Commun*, 9: 852). (7) The RING-type E3 ubiquitin ligase CLG1 can target GS3 for ubiquitination, leading to its degradation through the endosomal degradation pathway (Yang et al., 2021. *Mol Plant*, 14: 1699−1713). **(c) Optimizing the pleiotropic effects of IPA1.** *IPA1* is expressed in panicles and tiller bud tissues and regulates tiller number and spikelet number per panicle. A high expression level of *IPA1* promotes an increase in the number of spikelets per panicle. *An-1* encodes a previously reported domestication-related basic helix-loop-helix transcription factor that positively regulates awn length and negatively regulates spikelet number per panicle (Luo et al., 2013. *The Plant Cell*, 25: 3360−3376). An-1 binds to the promoter region of *IPA1* and suppresses its expression in panicle tissue, which reduces the spikelet number per panicle. Precise deletion of a 54-bp sequence with an An-1 binding site in the *IPA1* promoter region increases the number of grains per panicle and tiller number (Song et al., 2022. *Nat Biotechnol*, 40: 1403−1411).

Hd3a and *RFT1* for heading date, and *BPH29* regulating BPH resistance, are located within 0.3–3 Mb on chromosome 6. In addition, the NUE gene *OsTCP19* and the gelatinization temperature control gene *ALK* were tightly linked within 0.2 Mb, while the distance between *Pigm* for fungal blast resistance and *Hd1* for heading date was less than 1 Mb. Similarly, the chalkiness gene *Chalk5* is closely linked to the grain size genes *GS5* and *GW5*. Therefore, when integrating a target gene/allele from a specific donor germplasm, tightly linked unfavourable alleles may be simultaneously introduced into the end breeding product.

The close linkage of genes with diverse functions makes the design and breeding of targeted traits more complex. A precise genomic breeding scheme has been proposed to overcome this dilemma, which can quickly break the linkage within a minimum of 100 kb, significantly reducing field area, labor, and genotyping costs and achieving breeding goals within a few years [1]. Precise genome-wide editing techniques also provide a possible solution. For example, editing the promoter of *Wx* decreased the amylose content and enhanced rice quality without altering the closely linked *Hd3a* and *RFT1* genotypes [59]. Similarly, editing *TCP19* promoter enhanced NUE under low or moderate levels of nitrogen without changing the closely linked *ALK* genotypes [60]. Disruption of the GATA element of the *Chalk5* promoter can provide high-quality and consumer-desirable rice without affecting the *GW5* or *GS5* genotype [61].

Accelerating the creation of GSR via hybrid rice breeding
Over the past few decades, the yield potential of hybrid rice has increased by at least 20 %. In addition to the great contribution to the increase in yield, hybrid rice breeding could further facilitate the assembly of green genes in respective parental lines, therefore accelerating the integration of green traits twice as efficiently.

The breeding strategy of hybrid rice might be improved in three aspects: higher efficiency in outcrossing for introgression of a desired allele, better male sterility system for hybrid seed production, and increased yield potential by utilization of intersubspecific heterosis. Current cloning of a dominant genic male sterility gene, *SDGMS/OsRIP1*, can serve as an invaluable tool for facilitating outcrossing [62,63]. Using these genetic tools, designing and creating two complementary sets of effective genes in two parental lines may reduce the time cost relative to stacking all genes in a single genetic background. In addition, the genetic resources of cytoplasmic male sterility systems, such as CMS-WA, CMS-HL, CMS-BT, and CMS-FA [64–66], and environment-sensitive male sterility genes, such as *pms1*, *pms3/ptms12-1*, *cas/csa2*, and the most widely used *tms5*, greatly facilitate three-line and two-line hybrid systems, enabling large-scale commercial hybrid seed production [67]. On this basis, hybrid rice from intersubspecific crosses can lead to a 15–30 % greater yield advantage, by resolving postzygotic reproductive barriers such as hybrid sterility [68–72], and prezygotic reproductive barriers, such as the asynchronized diurnal floret opening time between subspecies [73].

Future prospects and international collaboration
Advancements in multiomics big data have already revolutionized rice breeding, which accelerate development of rice varieties that are more productive, resilient, and environmentally sustainable. One possible future direction involves leveraging gene-editing tools to precisely manipulate genetic traits, which allows for targeted modifications that can enhance desirable traits without the unintended consequences of traditional breeding methods. In addition, the cultivation of perennial rice is expected to become an important contributor to sustainable agriculture, which is especially beneficial for maintaining the ecological balance of terraced fields and fragile farmlands [74]. Furthermore, future genetic studies and breeding related to traits such as heat tolerance during the heading stage, photosynthetic efficiency, and herbicide resistance may also be important development directions.

Another promising avenue is the expansion of hybrid rice breeding programs. Hybrid rice varieties have demonstrated significantly higher yield potentials compared to traditional varieties, and the incorporation of GSR traits into these hybrids can amplify their benefits. Innovations in male sterility systems and the resolution of reproductive barriers between subspecies will be crucial in creating new hybrid combinations that maximize yield and stress resilience. This approach can effectively combine the strengths of different genetic backgrounds, accelerating the development of robust GSR varieties.

International collaboration is essential for the success of these initiatives. The challenges facing rice cultivation, such as climate change, pest and disease pressures, and the need for sustainable practices, are global issues that require coordinated efforts. Collaborative research programs, such as those spearheaded by the International Rice Research Institute (IRRI) and other international bodies, play a pivotal role in pooling resources, expertise, and genetic materials. These collaborations can facilitate the exchange of knowledge and technologies, ensuring that advancements in rice genetics and breeding are accessible to rice-growing regions worldwide. Moreover, international partnerships can help address the specific needs of different agro-ecological zones. By tailoring GSR varieties to local conditions,

such collaborations can ensure that the benefits of advanced breeding techniques are realized across diverse environments. Joint efforts in data sharing and the development of centralized databases, such as the Rice Gene Index [75] and RiceNavi [30], can enhance the ability of researchers to access and utilize multiomics data effectively. These resources enable breeders to make informed decisions, accelerating the selection process and improving the precision of breeding programs.

By harnessing the power of multiomics data, advancing hybrid rice breeding, and fostering international collaboration, the agricultural community can develop rice varieties that are not only high-yielding but also resilient to the challenges of the 21st century. These efforts will ensure that rice remains a cornerstone of food security for billions of people worldwide.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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