

ORIGINAL ARTICLE

Genetic diversity reveals synergistic interaction between yield components could improve the sink size and yield in rice

Khalid Anwar¹  | Rohit Joshi^{1,2}  | Alejandro Morales^{3,4,5} | Gourab Das¹ | Xinyou Yin³  | Niels P. R. Anten³ | Saurabh Raghuvanshi⁶ | Rajeev N. Bahuguna^{1,7} | Madan Pal Singh⁸ | Rakesh K. Singh⁹ | Martijn van Zanten⁴  | Rashmi Sasidharan⁵ | Sneh L. Singla-Pareek¹⁰  | Ashwani Pareek^{1,11} 

¹Stress Physiology and Molecular Biology Laboratory, School of Life Sciences, Jawaharlal Nehru University, New Delhi, India

²Division of Biotechnology, CSIR-Institute of Himalayan Bioresource Technology, Palampur, India

³Centre for Crop Systems Analysis, Plant Sciences Group, Wageningen University & Research, Wageningen, The Netherlands

⁴Molecular Plant Physiology, Institute of Environmental Biology, Utrecht University, Utrecht, The Netherlands

⁵Plant Ecophysiology, Institute of Environmental Biology, Utrecht University, Utrecht, The Netherlands

⁶Department of Plant Molecular Biology, University of Delhi South Campus, New Delhi, India

⁷Center for Advance Studies on Climate Change, Dr. Rajendra Prasad Central Agricultural University, Pusa, Samastipur, India

⁸Division of Plant Physiology, Indian Agricultural Research Institute, PUSA, New Delhi, India

⁹Crop Diversification and Genetics, International Center for Biosaline Agriculture, Academic City, Dubai, United Arab Emirates

¹⁰Plant Stress Biology, International Centre for Genetic Engineering and Biotechnology, New Delhi, India

¹¹National Agri-Food Biotechnology Institute, Mohali, India

Correspondence

Ashwani Pareek, Stress Physiology and Molecular Biology Laboratory, School of Life Sciences, Jawaharlal Nehru University, New Delhi 110067, India.
Email: ashwanip@mail.jnu.ac.in

Funding information

Netherlands Organisation for Scientific Research NWO, Grant/Award Number: 867.15.030 and 867.15.031; Department of Biotechnology, Ministry of Science and Technology, India, Grant/Award Number: BT/IN/NOW/15/AP/2015-16

Abstract

Intensive breeding programs have increased rice yields, strongly contributing to increasing global food security during the post-green revolution period. However, rice productivity has reached a yield barrier where further yield improvement is restricted by inadequate information on the association of yield components, and morphological and physiological traits with yield. We conducted a field experiment to evaluate (i) the contribution of morphological and physiological traits to yield and (ii) quantify the trade-off effect between the yield components in rice, using a mini-core collection of 362 rice genotypes comprising geographically distinct landraces and breeding lines. Our data point towards multiscale coordination of physiological and morphological traits associated with yield and biomass. Considerable trait variations across the genotypes in yield ranging from 0.5 to 78.5 g hill⁻¹ and harvest index ranging from 0.7% to 60.7% highlight enormous diversity in rice across the globe. The natural elimination of trade-off between yield

Khalid Anwar and Rohit Joshi equally contributed.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Food and Energy Security* published by John Wiley & Sons Ltd.

components revealed the possibility to enhance rice yield in modern cultivars. Furthermore, our study demonstrated that genotypes with larger sink sizes could fix more carbon to achieve a higher yield. We propose that the knowledge thus generated in this study can be helpful for (a) trait-based modeling and pyramiding alleles in rice-breeding programs and (b) assisting breeders and physiologists in their efforts to improve crop productivity under a changing climate, thus harnessing the potential for sustainable productivity gains.

KEYWORDS

biomass, genetic diversity, grain yield, phenotyping, rice, sink size, traits, yield barrier

1 | INTRODUCTION

Rice is a staple cereal crop for more than half of the global population (Fukagawa & Ziska, 2019). It is envisaged that additional 112 million metric tons of rice will be required by 2035 to feed the growing population (Seck et al., 2012). This yield increase must be achieved against a backdrop of shrinking arable land area, depleting water resources, and increasing climatic variation (Wang et al., 2018). However, growth in rice production has slowed down from 2.7% per year in 1970–1990 to 1.2% per year in 1990–2007 (Ray et al., 2012; Wassmann et al., 2009). In major rice growing regions, yield stagnancy may be due to a combination of location-specific factors including high day and night temperature, poor soil fertility, problematic soil, limiting water resources, and increased incidences of pest and diseases (Ray et al., 2012; Zhao et al., 2017). In addition, poor access to credit and low crop prices are also suggested as contributors to yield stagnancy of rice and wheat in Asia and Australia (Erenstein, 2012; Tanaka et al., 2015). There is, therefore, an urgent need to introduce improved crop varieties that are climate-smart and high(er) yielding (Dayton, 2014) that could overcome the existing yield barrier. To help breeders meet these challenges, the assessment and classification of the existing genetic and phenotypic diversity of rice within domesticated populations and wild relatives are required (Ebana et al., 2010; Jin et al., 2010; Wang et al., 2014). This is particularly relevant because besides being a primary food source for a large part of the world population, rice is also an excellent monocot model system for crop genomics (Gutaker et al., 2020; Kumari et al., 2009; Spindel et al., 2016; Wang et al., 2014). In this regard, assessing the interaction between genotype and phenotype in rice becomes a central goal, as it facilitates the efficient development of novel varieties in a knowledge-based manner (Pareek et al., 2020).

Various reports on enhancing biomass and yield by manipulating physiological and morphological traits in diverse crop species have demonstrated enormous potential

to improve biomass and yield (Jones et al., 2015; Qu et al., 2017). However, it is essential to understand the genetic basis (e.g., genes, SNPs, QTLs) of phenotypic traits and their interaction to contribute to adaptability and increased yield potential across the environmental conditions and cultivation practices (Khush, 2001; Wang et al., 2018). High-throughput genotyping has led to the identification and characterization of genome-wide genetic markers in genotypes/mapping populations, along with a large number of loci that were mapped to understand the genetic regulation of plant growth and yield (Chen et al., 2014a, 2014a; Davey et al., 2011; Huggins et al., 2019; Kadam et al., 2017, 2018). However, systematic assessments that allow for the quantification of plant phenotypes underlying dynamic processes in crops, such as the contribution of individual traits to improve biomass and yield, are still lagging (Chen et al., 2014a, 2014b; Furbank et al., 2019; Houle et al., 2010). Hence, to improve rice cultivars through genetic engineering or conventional breeding, the current major challenge is defining the interaction of physiological and morphological traits associated with enhanced biomass production and grain yield (Qu et al., 2017).

The development of new and improved varieties with desirable traits in any cultivated plant species by traditional breeding (artificial selection) depends primarily on the diversity represented in the germplasm (Fatokun et al., 2018). Collection, curation, and conservation of genotypes provide resources of potentially valuable material to plant breeders (Mascher et al., 2019). During the past decades, extensive efforts have been made at the global level to collect and maintain the germplasm of crop species and their close relatives in international gene banks (Gruber, 2017). These genotypes represent a valuable reservoir of genetic resources for the desired traits for breeding. However, exploitation of these collections requires comprehensive systematic and large-scale phenotypic and genotypic evaluations (Ford-Lloyd et al., 2001). Nevertheless, genetic diversity for the traits determining sink size reveals the natural potential of existing germplasm to break the

existing yield barrier and characterizes these traits to further enhance the yield of existing elite cultivars. Grain yield is dependent on both the source and the sink capacity, which are interdependent (Dingkuhn et al., 2020). The sink depends on the source for photo-assimilate supply while the efficiency of the source is regulated by the sink size and activity (Bahuguna et al., 2017; Koch, 2004). It has been reported that larger sink size (defined as number of spikelets $m^{-2} \times 1000$ -grain weight) is required to produce a higher yield in rice (Lubis et al., 2003). However, inherent trade-offs between yield components are a major bottleneck to achieve a larger sink in crops such as rice. Conversely, the grain-filling stage is considered as the most critical stage to achieve higher yield under optimum conditions, where sink activity and size play a crucial role (Dingkuhn et al., 2020; Koch, 2004).

More than 130,000 distinct rice varieties are currently recognized worldwide, and most of these are underexplored in terms of systematic trait analysis (Vaughan et al., 2008; Wang et al., 2014). Moreover, germplasm “mini core” and “core” collections have been developed, representing the maximal genetic diversity with minimum redundancy (Fatokun et al., 2018; Upadhyaya & Ortiz, 2001; Zhang et al., 2014). In this study, we cultivated 362 rice mini-core lines under field conditions during the rice cropping season in India (New Delhi) to explore (i) phenotypic variation in morphological and physiological traits critical to growth, biomass, and yield (Table 1) and (ii) correlation among yield components leading to improved sink size and yield. Our detailed dataset will be helpful to predict the performance of rice genotypes, which can be further exploited and utilized in breeding for higher yield in an optimal environment. Moreover, it can provide a platform for mining natural alleles for genetic improvement of varieties for improved biomass and yield.

TABLE 1 Traits, their abbreviations, and units as used in the study

Traits	Abbreviations	Units
Plant Height	PH	centimeter (cm)
Chlorophyll content (Veg)	SPAD (Veg)	number
Days to flowering	DTF	days
Number of Tillers per hills	Tillers	number
Chlorophyll content (Flag)	SPAD (Flag)	number
Number of Panicles per hill	Panicles	number
Panicle length	PL	cm
Number of spikelets per panicle	SPP	number
Grain weight	GW	gram (g)
Total yield	TY	gram (g)
Harvest index	HI	percentage (%)
Fresh weight of whole plant	FW	gram (g)
Dry weight of whole plant	DW	gram (g)

2 | MATERIALS AND METHODS

2.1 | Rice genotypes and growth conditions

Three hundred and ninety-four (394) accessions of rice genotypes were procured from the International Rice Gene Bank, maintained by IRRI (<https://www.irri.org/international-rice-genebank>) (Table S1). These genotypes represent the “mini-core” collection of >130,000 rice accessions (cultivars and landraces) and wild relatives. This minicore was subdivided according to Garris et al. (2005) and includes *indica* (75), *aus* (53), *aromatic* (16), *temperate japonica* (100), *tropical japonica* (86), and *admixed* (64) accessions in view of evolutionary relationships between *indica* (144) and *japonica* (186). The geographical information about these core collections, representing more than 80 countries (Figure 1), are derived from IRRI's online database (<https://www.genesys-pgr.org>).

To carry out the phenotyping of morphological and physiological traits, the 394 rice genotypes were grown under field conditions at New Delhi, India (28° 38'23"N, 77° 09'27"E, 228.61 m above mean sea level), during the “Kharif” season (i.e., June–October) (Figure S1). The growth conditions were semiarid with daily temperatures during summer reaching up to 44°C. Relative humidity ranged from 40% to 85% with an average 900–1200 mm annual rainfall (IARI Metrological Database System). Thirty-two of the 394 genotypes in the collection did not germinate or did not reach the flowering stage under these conditions. Therefore, phenotyping was restricted to the remaining 362 accessions. Table S2 contains all the data collected during this study.

Rice seedlings were raised in a field nursery using the dry-bed method (<http://www.knowledgebank.irri.org/>).

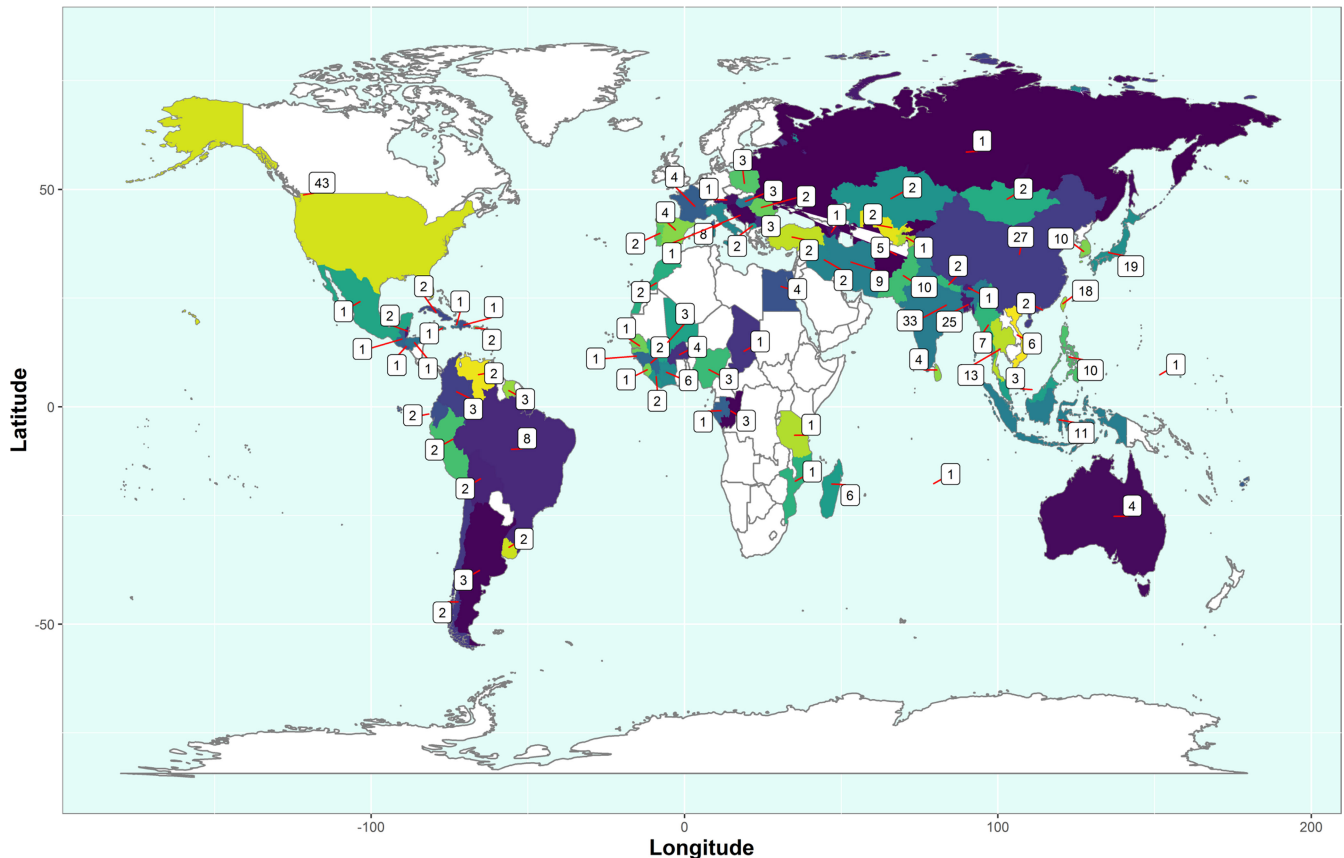


FIGURE 1 Map showing the geographical location of the 394 rice accessions used in this study: The countries from where the rice accessions were originally collected are colored. Numbers in the boxes represent the total number of genotypes collected from a particular country

The nursery was irrigated regularly to maintain the moisture level in the soil. To provide adequate nutrition to the developing seedlings, the upper layer of the soil was mixed with vermicompost (0.9 kg m^{-2}) and urea (1 g m^{-2}), diammonium phosphate (2 g m^{-2}), and muriate of potash (1 g m^{-2}), respectively. Twenty-one-days-old seedlings were then transplanted with two seedlings hill^{-1} in the puddled field arranged in a randomized complete block design with an alpha lattice pattern in three replicates. The between-rows and within-rows spacing was $25 \times 25 \text{ cm}$. Each genotype was sown in three rows, with five hills per row in a replicate resulting in 1182 plots across the three replicates. However, only five central hills were taken from the plot of each genotype to record the phenotypic data and yield component analysis, while the border rows were excluded. Urea (N), single superphosphate (P), and muriate of potash (K) were applied at the rate of 120, 40, and 60 kg ha^{-1} , respectively. The entire dose of P and K fertilizers was applied as basal dose while N fertilizer was applied in three splits, that is, 50% before transplanting, 25% at active tillering, and the remaining 25% when a majority of genotypes was close to the heading stage. No major insect and pest infestation was observed during the experiment.

2.2 | Observations and recording of phenotypic traits

2.2.1 | Greenness index (SPAD)

Greenness index (SPAD value) was measured using a self-calibrating SPAD-502 chlorophyll meter (Konica Minolta Inc.) based on leaf transmittance at 650 nm (red) and 940 nm (IR) wavelengths. All the Soil Plant Analysis Development (SPAD) measurements were recorded on the third uppermost leaf during the vegetative phase [SPAD(Veg)] and the flag leaf during the reproductive phase [SPAD(Flag)] between 09:00 and 11:30 h, randomized across genotypes. Three replicate readings were taken on one side of the leaf's midrib and averaged for a single observation (Yang et al., 2014).

2.2.2 | Yield and yield components

Plant samples were harvested at maturity. Five hills were harvested from the middle rows of each genotype in each replication to avoid any confounding border effects. The number of tillers and panicles were counted manually for

each hill. Days to flowering (DTF) was calculated as duration from the sowing to the 50% flowering stage of the respective genotype and averaged across the replicates. Plant height (PH) was measured as the distance from the base to the tip of the topmost flag/upper leaf and expressed in centimeters. The number of spikelets (fertile) panicle⁻¹ was also estimated. Panicles were separated from all the harvested samples, and the straw was oven-dried at 70°C until a constant weight was obtained. The straw dry weight (DW) was included in the calculation of total biomass. The panicles were sun-dried in net bags and weighed using an analytical balance (model: BSA124S-CW, Sartorius AG). Grain yield was determined for each hill and adjusted to the standard moisture content of 14% (Bahuguna et al., 2017). The above-ground total biomass was the combined dry matter of straw and panicles. Thousand grain weight was calculated by weighing three replicate samples of 1000 grains, each taken randomly for each genotype. The number of spikelets (fertile) were estimated in each panicle separately. Harvest index was calculated as the ratio of grain yield (in DW) to the total above-ground biomass (Sinclair, 1998).

2.3 | Statistical analysis

Traits data were collected from the field in triplicates, and all the statistical analyses were done using R statistical software (version 3.6.0). For each trait, to check how field data vary across the genotypes, one-way ANOVA was performed using *ggpubr* (version 0.2.4) on log-transformed (natural logarithm) values (Table S3). To reduce Type-I error, *p*-values were adjusted using a Bonferroni correction. To explore the contribution (in percentage) of each trait on data variability, principal component analysis (PCA) was conducted on log-transformed data of all traits by *FactoMineR* (version 2.2) and *Factoextra* (version 1.0.6) packages after scaling each trait to unit variance. Also, to know the interrelationships/dependencies among the traits, correlation analysis based on log-transformed data was carried out using R base packages (Table S4).

3 | RESULTS

3.1 | The rice mini-core collection exhibits high phenotypic diversity

We observed significant variability ($p < 0.001$) for all the phenotypic traits across the genotypes (Figure S2). Significant variation was observed in the greenness index (SPAD value) of the flag leaf with genotypic mean SPAD

values ranging from 22.0 (RTS 4) to 57.9 (Saku). Besides, we observed that some of the genotypes, such as Ligerito, Miriti, and Saku, displayed a high greenness index at the vegetative and reproductive stage and stayed green even at the physiological maturity stage. In contrast, some of the genotypes, such as IR8, OS6, and KPF16, consistently showed low SPAD values. The phenotypic diversity in the minicore is shown in the form of violin plots in Figure 2. DTF varied from 68 days in Pappaku to 150 days in JM70. PH ranged from 44.5 cm in Aijiaonante to 197.0 cm in Gogolempuk, while above-ground fresh weight (FW) was highest in Coarse (515.8 g hill⁻¹) and lowest in Bulgare (14.1 g hill⁻¹) (Table S2). Aboveground DW was highest in Tog 7178 (339.8 g hill⁻¹) and lowest in Kaw Luyoeng (1.5 g hill⁻¹). Panicle length (PL) varied from 10.6 to 38.1 cm (Figure 2). Significant variations were observed in the tiller number hill⁻¹ among different genotypes, ranging from 2 (Biser 1, IRAT 44, Norin 20, Saku) to 41 (Yodanya). The number of panicles hill⁻¹ (Panicles) ranged from 1 (DK 12 and Saraya) to 38 (Yodanya), and spikelets panicle⁻¹ (SPP) varied from 3.8 (Vavilovi) to 345.5 (Trembese), with an average of 93.2. The Grain weight (GW) varied from 8.32 (Saraya) to 45.42 g (Lusitano) with an average of 26.1 g. The total grain yield hill⁻¹ (GY) ranged from 0.5 g hill⁻¹ (Saraya) to 78.5 g hill⁻¹ (9524) with an average of 19.3 g hill⁻¹. The harvest index (HI) ranged from 0.7% (CO18) to 60.7% (ARC 10086) (Figure 2 & Figure S3).

3.2 | Multivariate evaluation of phenotypic parameters using Principal Component Analyses

Principal component analyses was performed to assess relative contributions to global phenotypic variation within the population and to estimate the contribution of individual traits and their combinations to variation in biomass and yield (Figure 3 and Figure S4). The PCA showed that GY, SPP, FW, and DW contributed the most, and GW had the least contribution to the observed variability across the genotypes (Figure 3A). Figure 3B shows that the genotypes with high yield and biomass mainly belong to *aus* and *indica* subgroups. GY, SPP, Tillers, and Panicle numbers clustered together, indicating a high correlation among them, which was reconfirmed by correlation analysis (Figure 4). Similarly, FW, DW, PH, and PL clustered together, indicating a correlation between these traits, which is also evident from Figure 4. GW, Tillers, Panicle numbers, FW and DW clustered in opposite directions, indicating a negative correlation, whereas vegetative stage and flag leaf chlorophyll content (SPAD) showed a positive correlation.

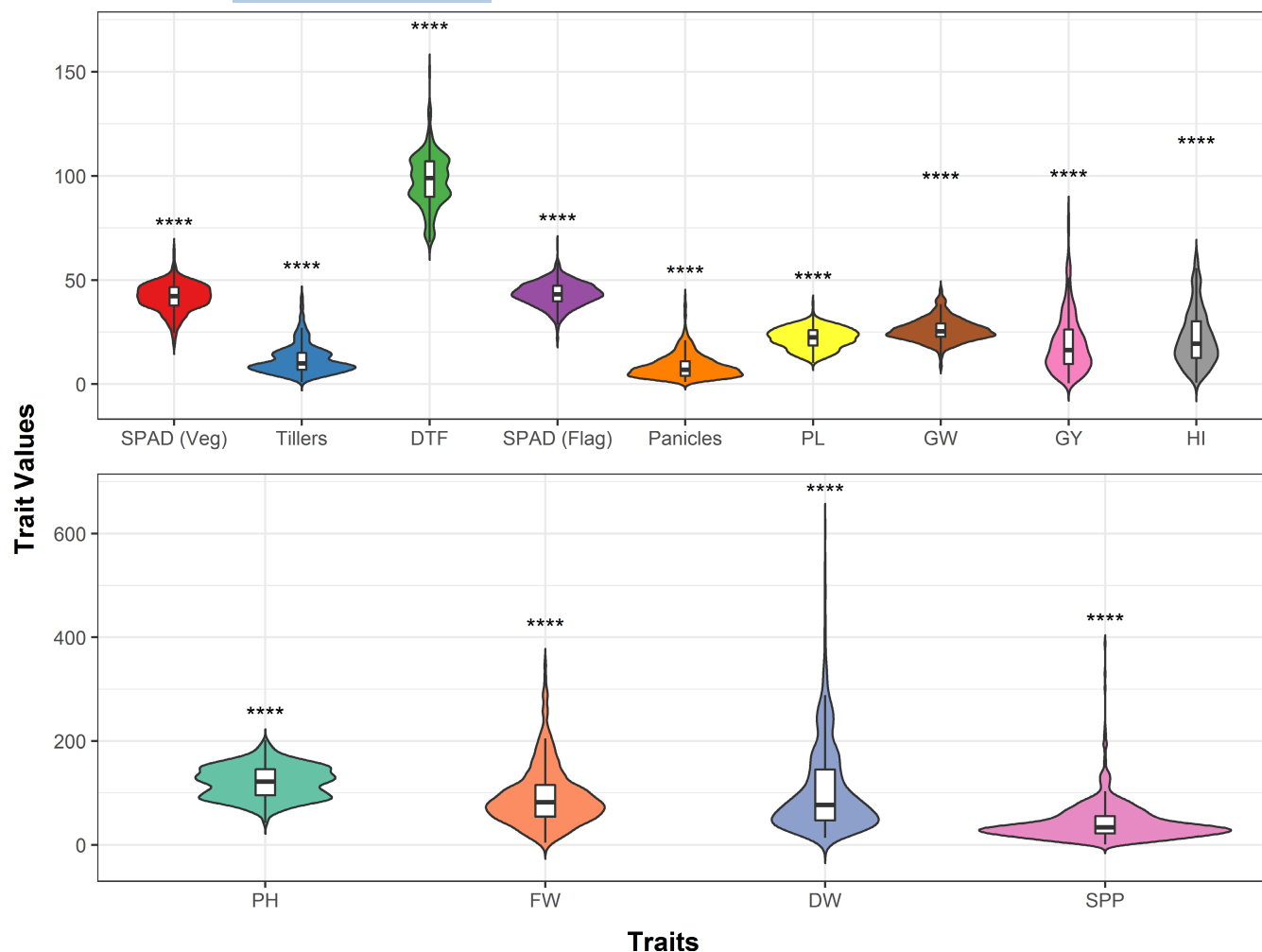


FIGURE 2 Violin plot showing phenotypic diversity in the rice mini-core collection: X- and Y-axes show different measured traits and the corresponding trait values for individual plants, respectively. Plotted are all median values ($n = 3$) for each trait of the 362 individual accessions, and significance values shown are from ANOVA (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and **** $p < 0.0001$). The vertical and horizontal axes of the violin plot showing the distribution and probability density of the data, respectively. White boxes represent interquartile ranges, with the black horizontal lines representing the median. Whiskers indicate spread to the highest and lowest data point

3.3 | Correlation among traits

The correlation coefficients and data distributions among the 13 measured traits (Table S2) are shown in Figure 4. Yield can be decomposed via two equations, either from total DW (as $\text{Yield} = \text{DW} \times \text{HI}$) or the yield components (as $\text{Yield} = \text{tillers hill}^{-1} \times \text{panicles tiller}^{-1} \times \text{spikelets panicle}^{-1} \times \text{GW}/1000$), knowing that there is one grain per fertile spikelet (only fertile spikelets were recorded). Yield components were not highly correlated with each other (Figure 4), making them ideal to understand where the variation in yield across genotypes originates from. Based on the correlation of each yield component with the yield itself, it appears that the number of tillers per hill and an average number of fertile spikelets per panicle are the most critical drivers of variability in yield and, to a lesser extent, the average number of panicles per tiller (this is a measure of the fraction of productive tillers). On the other

hand, there was a weak correlation between yield and grain weight (which also had a minor variation compared to the other yield components). When using DW and HI to explain yield, the analysis shows that both traits are important. HI was strongly correlated with the average number of fertile spikelets per panicle but not correlated to any other yield components (Figure 4).

Pearson correlation coefficients were determined to evaluate the correlation of yield (Figure 5A) and biomass (Figure 5B) hill^{-1} with the other traits. The results demonstrate that PH (0.30), tillers (0.41), panicles (0.58), PL (0.49), DTF (0.21), SPP (0.68), GW (0.03), HI (0.54), FW (0.60), and DW (0.46) positively correlated with the yield, whereas SPAD (Veg) showed a negative correlation (Figure 5A). On the other hand, PH (0.47), tillers (0.38), panicles (0.47), PL (0.48), DTF (0.28), SPP (0.18), FW (0.80), and GY (0.46) showed a positive correlation with biomass (Figure 5B).

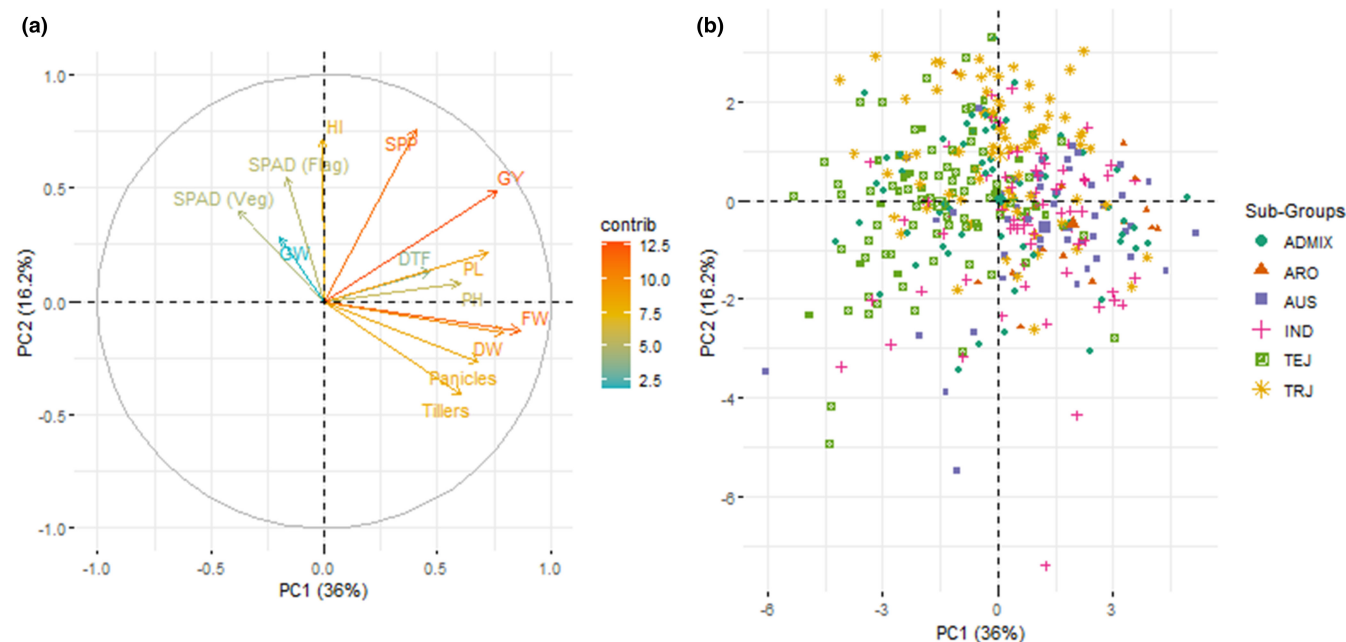


FIGURE 3 Contribution of different variables in PCA of the overall dataset: (a) Biplot showing the first two principal components (PC1 and PC2), the variance they explain (52.2%), and relationships among the traits measured. The contribution to the total variance of each trait is shown with a color scheme provided in the figure. (b) PCA plot showing the contribution of rice subspecies to the total variance in this study (see Figure S4). Rice genotypes used in this study are grouped into six subspecies, that is, ADMIX (a mixture of indica and japonica), ARO (Aromatic), AUS (Aus-indica), IND (Indica), TEJ (Temperate japonica), and TRJ (Tropical japonica)

3.4 | Genetic response for the traits contributing to sink size and yield barrier

Genetic diversity recorded for three component traits (panicles hill⁻¹, spikelets panicle⁻¹, and grain weight) that directly contribute to sink size at grain filling stage and final yield revealed significant ($p < 0.001$) variation ranging from 454.8 to 84181.5 mg hill⁻¹ in sink size and 0.5 to 78.5 g hill⁻¹ in yield (Figure S5, Table S2). We have further evaluated 50 of these genotypes based on their larger sink size. A strong trade-off was observed between panicles hill⁻¹, spikelets panicle⁻¹, and grain weight for the majority of genotypes (Figure 6). Interestingly, only three genotypes Tog 7178 (Admixed), 923 (Admixed), and PADI PAGALONG (Tropical Japonica), showed positive interaction between panicles hill⁻¹, spikelets panicle⁻¹, and grain weight and recorded the highest values of all three traits, predicting three to four times bigger sink size as compared to the average sink size of the “mini-core” population (Figure 7).

4 | DISCUSSION

Global rice production needs to be increased up to 50% to feed the growing population by 2050 (Roos et al., 2017). However, the growth rate in rice productivity has slowed down in the past three decades. Moreover, climate change

and limited land and water resources pose an increasingly serious threat to achieving the required target in rice production. Higher grain yield and biomass are the two most important agronomically desired targets of the breeding programs (Qian et al., 2016). Understanding the relation of diverse morphological and physiological traits with yield parameters can be very useful since a strong correlation with grain yield could be exploited to use these traits as an indirect selection criterion for breeding better yielding cultivars. For example, studies have shown that while small plants have high productivity, taller individuals acquire more light share in competition, a phenomenon known as “tragedy of the commons” (Anten & Vermeulen, 2016). Therefore, the development of semidwarf varieties is considered important for rice breeding. This trait has played a significant role in developing high-yielding rice varieties during the green revolution (Mooney, 2009; Palme et al., 2014). In this study, we have done a systematic assessment of the phenotypic variations in different growth and yield traits in a rice diversity panel of 362 accessions. We scored 13 diverse morphological and physiological traits in plants brought to maturity under field conditions employing the standard agronomic practices.

We identified several genotypes which have dwarf or semidwarf phenotype ranging from 44.5 to 99.0 cm in PH. On the other hand, we also identified several tall genotypes ranging from 150 to 197 cm. Tillering in rice is reported as a major determinant of canopy architecture, grain yield,



FIGURE 4 Correlation graphs of physiological, morphological, yield, and biomass parameters: Lower left panels: Scatter plots of each trait against each other, with a robust linear regression (red), line plotted on it. Diagonal panels: Density plots representing the distribution of values for each trait, with the red text representing median and interquartile range (IQR) for each trait. Median and IQR are analogous to mean and standard deviation but are more informative when distributions are skewed and in the presence of outliers, which is the case for these data. Upper right panels: Kendall's tau coefficient per comparison, a nonparametric version of the correlation (Corr) coefficient (more robust against outliers and more informative when the data are not normally distributed). This coefficient varies between -1 and 1 as the canonical correlation coefficient. A color system is used to represent the strength of the correlation, with a positive correlation in red and a negative correlation in blue

and biomass (Barnaby et al., 2019; Xu et al., 2020). Our results showed a significant variation among the genotypes in the number of tillers hill^{-1} , with an average of 12 tillers genotype^{-1} . Panicle length also determines grain number and grain yield in rice (Ikeda et al., 2010). Our study shows considerable diversity in the panicle number hill^{-1} among the mini-core rice accession that we screened.

4.1 | A complex interaction of yield components reveal the potential to enhance rice yield

We found a strong correlation between HI and yield. Higher HI indicates the enhanced allocation of photosynthate to the grains (Jiang et al., 2018) and relatively

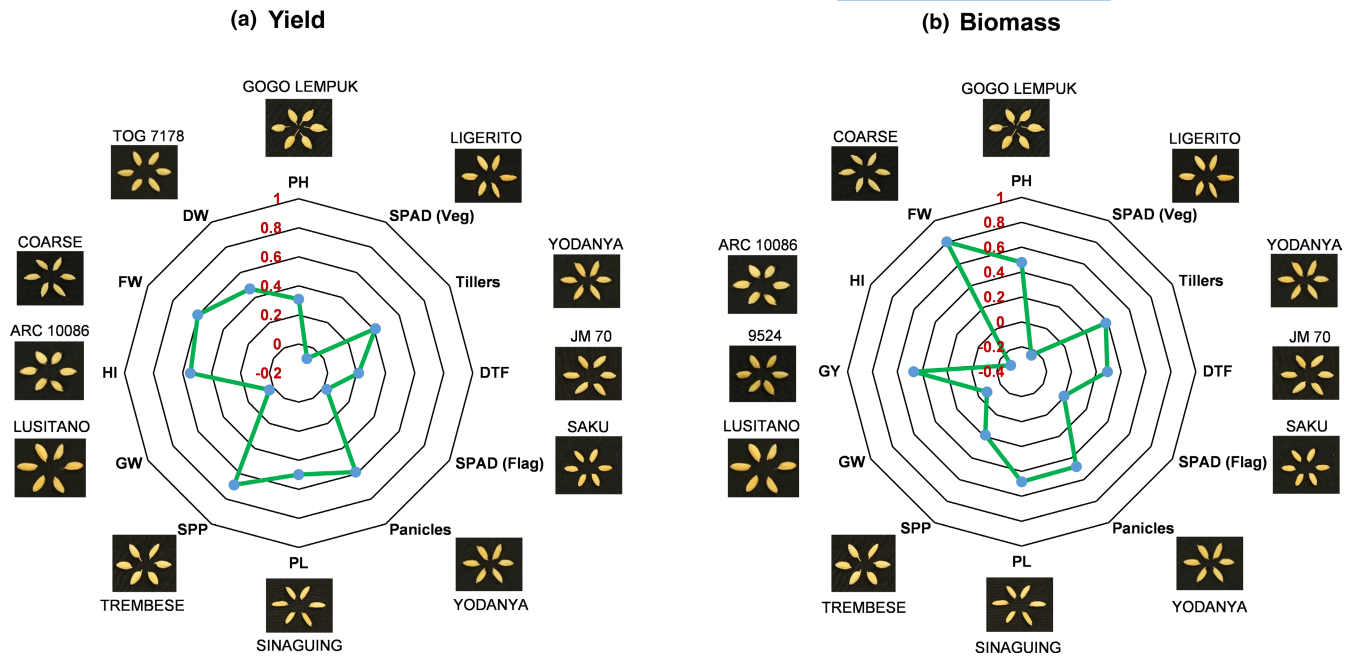


FIGURE 5 Graphical representation of correlations between the measured traits in the 362 rice genotypes with (a) yield and (b) biomass. (a) All traits positively correlated with yield, except the SPAD value (Veg). (b) SPAD value (Veg), SPAD value (Flag), harvest index (HI), and grain weight (GW) showed a negative correlation with biomass while plant height (PH), tillers, DTF, panicles, panicle length (PL), spikelets panicle⁻¹ (SPP), grain yield (GY) and FW positively correlated with biomass. For each trait, the accession name and image of six representative seeds of the best performing genotype are shown in the outer circle



FIGURE 6 Venn diagram showing the distribution of genotypes and shared trait responses (panicles hill⁻¹, spikelets panicle⁻¹ (SPP), and grain weight (GW)) from top 50 performing rice genotypes out of 362 mini-core collection. Numbers correspond to genotypes present in individual and shared traits

less to resource harvesting structures, leaves, stems, and roots. In natural systems, populations with high HI and high population-level seed production are prone to invasion by genotypes that invest relatively more in resource harvesting, as these will acquire more of the available resources, dubbed a “tragedy of the commons” (TOC, Anten & Vermeulen, 2016). This conflicts with the goal in agriculture to increase production per area, and this has led to the idea that yields can be enhanced by generating plants that optimize their assimilate partitioning by developing a communal ideotype by reducing “growth

redundancy” (Donald, 1968; Zhang et al., 1999). Previous reports have shown that modern varieties of several crops exhibit various traits that run counter to this TOC and significantly contributed to yield, such as shorter stature in several crops, smaller less-branched roots in maize and wheat, vertical leaves, reduced leaf senescence in maize, and smaller leaves in cotton (Anten & Vermeulen, 2016). Further, flowering time is another vital trait closely associated with yield-related traits as plants achieve reproductive competency after accumulating the desired amount of photoassimilates in the vegetative sink (Smith et al., 2018). Thus, plant architecture plays a critical role in achieving reproductive competency and entering the flowering stage (Teichmann & Muhr, 2015). Significant variations were observed in time (days) to 50% flowering, and a positive correlation was obtained between DTF and grain yield. Previous studies have also found a positive correlation between days to heading and grain yield in rice (Rashid et al., 2014).

Previous workers grouped several rice genotypes into different clusters based on various morphological characters (Ahmadikhah et al., 2008) and physiological traits (Tuhina-Khatun et al., 2015). The 13 phenotypic traits monitored in this study have been used routinely to correlate species diversification rates and phenotypic divergence in micro- and macro-evolutionary studies (Armbruster et al., 2004; Eble, 2004; Ricklefs, 2004, 2006). Breeding by pyramiding favorable alleles of the

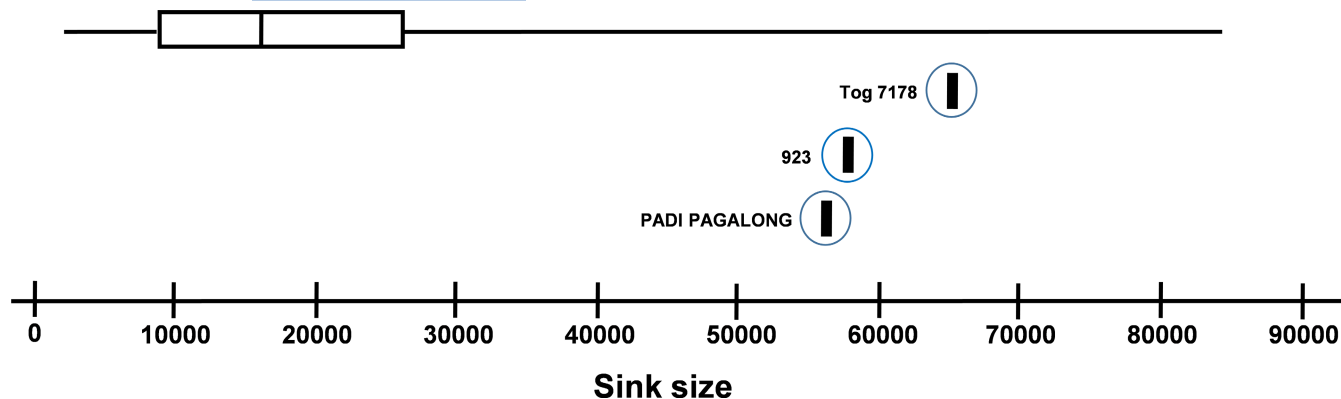


FIGURE 7 Box plots showing genotypes having different sink sizes (mg hill^{-1}): Genotypes (Tog 7178, 923, and PADI PAGALONG) having positive interaction between panicles hill^{-1} , spikelets panicle^{-1} , and grain weight and recorded the highest values of all three traits

corresponding clusters is a feasible strategy for biomass and yield improvement. However, such a pyramiding of genes may act differently beyond estimated predictions. This could be analyzed through trait-based modeling in rice-breeding programs (Rohila et al., 2019) and a well-designed integrated breeding strategy considering all related traits must be part of future rice breeding programs (Tan et al., 2020). Our study presents previously untapped phenotypic variations in available germplasm that can be used to improve biomass and productivity in rice to meet increased demands (Chen et al., 2016; Rohila et al., 2019). Also, researchers worldwide can leverage the phenotypic information documented here for efficient utilization in association mapping of available rice germplasm.

4.2 | A larger sink size could enhance rice yield in the future environment

Crop productivity is determined by season-long canopy photosynthesis, which depends on factors like leaf-level photosynthesis as well as canopy size or leaf area index. Previous studies have suggested that regulating photosynthetically active leaf area during different growth stages is an effective strategy for improving crop production (Acosta-Motos et al., 2017). Furthermore, large-scale surveys done in previous studies demonstrated that new breeding programs involve improved canopy photosynthesis to enhance biomass and yield (Hubbart et al., 2007; Peng et al., 2001). After investigating 14 photosynthesis-related parameters using 215 USDA-curated global mini-core accessions and Chinese cultivars, it was demonstrated that the photosynthetic rate under low light was correlated with biomass (Qu et al., 2017). Thus, photosynthesis plays a significant role in enhancing crop biomass and yield potential (Zhu et al., 2010). One of the major challenges to enhance biomass production and yield is,

thus, to enhance photosynthesis. However, translating the contribution of higher photosynthesis (photoassimilate production) into biomass and yield would require a larger sink size and efficient translocation of photosynthate to the developing sink (grains) (Dingkuhn et al., 2020). Moreover, being a C3 plant, rice genotypes with larger sink size might benefit from higher carbon fixation under rising CO_2 (Ziska et al., 2012). Previous carbon dioxide enrichment studies showed that enhanced supply of substrate (CO_2) increased photosynthesis, which eventually increased yield in wheat and rice genotypes (Chaturvedi et al., 2017; Driever et al., 2014). However, genotypic variation in leaf photosynthesis did not show a direct correlation with yield (Dingkuhn et al., 2020; Driever et al., 2014), which could be attributed to the smaller sink at vegetative and/or grain filling stage. This sink limitation feeds back on the photosynthetic rate, limiting the production of photoassimilate. Thus, larger sink may allow continued supply of photo-assimilates to enhance yield. In this study, we observed significant genetic diversity in key traits that determine the sink size at the grain filling stage. For example, the number of panicles hill^{-1} , spikelet number panicle^{-1} , and individual grain weight varied significantly, but their contribution to grain yield was limited by an increase in the trait at the cost of the other two. Existing trade-off between yield components has been reported as the major bottle-neck to improve yield in crop breeding programs (Dingkuhn et al., 2020; Mora-Ramirez et al., 2021). For example, an increase in grain size did not increase yield in wheat due to potential trade-off between grain size and grain number (Mora-Ramirez et al., 2021). We have selected the top 50 high-yielding genotypes and observed the pattern of these three traits and their contribution to the sink size and grain yield. Interestingly, only three genotypes showed synergistic changes in three traits resulting in significantly higher grain yield ($53.3\text{--}63.0 \text{ g hill}^{-1}$) and harvest index ($15.1\text{--}55.7\%$). This critical

observation indicated the plausible route to design crops that may exhibit larger sinks and, thus, benefit from a potential increase in photosynthesis through breeding programs or rising ambient CO₂ in future climate. Moreover, the genotypic variation in sink size and its association with higher yield under optimum environment would provide a platform for mining natural alleles responsible for determining sink size and strength.

ACKNOWLEDGMENT

AP and SLS-P would like to thank the support received from the Department of Biotechnology, Government of India, for the Indo-NWO Project (BT/IN/NOW/15/AP/2015-16). This research was funded by the Netherlands Organisation for Scientific Research (NWO), project numbers 867.15.030 (AM, NA, and XY) and 867.15.031 (AM, RS and MvZ).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS


AP conceptualized the idea of the study. KA and RJ performed most of the experiments. AM, GD, and RNB helped in analyzing data. KA and RJ wrote the manuscript. XY, NPA, SR, MPS, RKS, MZ, RS, SLS-P, and AP participated in the writing and editing of the manuscript. All authors have read and approved the manuscript.

ORCID

Khalid Anwar  <https://orcid.org/0000-0002-5425-2460>

Rohit Joshi  <https://orcid.org/0000-0002-6524-4722>

Xinyou Yin  <https://orcid.org/0000-0001-8273-8022>

Martijn van Zanten  <https://orcid.org/0000-0002-2810-7374>

Sneh L. Singla-Pareek  <https://orcid.org/0000-0002-0521-2622>

Ashwani Pareek  <https://orcid.org/0000-0002-2923-0681>

REFERENCES

- Acosta-Motos, J. R., Ortuno, M. F., Bernal-Vicente, A., Diaz-Vivancos, P., Sanchez-Blanco, M. J., & Hernandez, J. A. (2017). Plant responses to salt stress: Adaptive mechanisms. *Agronomy*, 7(1), 18. <https://doi.org/10.3390/agronomy7010018>
- Ahmadikhah, A., Nasrollanejad, S., & Alishah, O. (2008). Quantitative studies for investigating variation and its effect on heterosis of rice. *International Journal of Plant Production*, 2(4), 297–308.
- Anten, N. P., & Vermeulen, P. J. (2016). Tragedies and crops: Understanding natural selection to improve cropping systems. *Trends in Ecology & Evolution*, 31(6), 429–439. <https://doi.org/10.1016/j.tree.2016.02.010>
- Armbruster, W. S., Pelabon, C., Hansen, T. F., & Mulder, C. P. H. (2004). Floral integration, modularity and accuracy: Distinguishing complex adaptations from genetic constraints. In M. Pigliucci, & K. Preston (Eds.), *Phenotypic integration: Studying the ecology and evolution of complex phenotypes* (pp. 23–49). Oxford University Press.
- Bahuguna, R. N., Solis, C. A., Shi, W., & Jagadish, K. S. (2017). Post-flowering night respiration and altered sink activity account for high night temperature-induced grain yield and quality loss in rice (*Oryza sativa* L.). *Physiologia Plantarum*, 159(1), 59–73. <https://doi.org/10.1111/ppl.12485>
- Barnaby, J. Y., Pinson, S. R., Chun, J., & Bui, L. T. (2019). Covariation among root biomass, shoot biomass, and tiller number in three rice populations. *Crop Science*, 59(4), 1516–1530. <https://doi.org/10.2135/cropsci2018.09.0595>
- Chaturvedi, A. K., Bahuguna, R. N., Shah, D., Pal, M., & Jagadish, S. V. K. (2017). High temperature stress during flowering and grain filling offsets beneficial impact of elevated CO₂ on assimilate partitioning and sink-strength in rice. *Scientific Reports*, 7, 8227. <https://doi.org/10.1038/s41598-017-07464-6>
- Chen, D., Neumann, K., Friedel, S., Kilian, B., Chen, M., Altmann, T., & Klukas, C. (2014a). Dissecting the phenotypic components of crop plant growth and drought responses based on high-throughput image analysis. *The Plant Cell*, 26(12), 4636–4655. <https://doi.org/10.1105/tpc.114.129601>
- Chen, W., Wang, W., Peng, M., Gong, L., Gao, Y., Wan, J., Wang, S., Shi, L., Zhou, B., Li, Z., Peng, X., Yang, C., Qu, L., Liu, X., & Luo, J. (2016). Comparative and parallel genome-wide association studies for metabolic and agronomic traits in cereals. *Nature Communications*, 7, 12767. <https://doi.org/10.1038/ncomm512767>
- Chen, X., Cui, Z., Fan, M., Vitousek, P., Zhao, M., Ma, W., Wang, Z., Zhang, W., Yan, X., Yang, J., Deng, X., Gao, Q., Zhang, Q., Guo, S., Ren, J., Li, S., Ye, Y., Wang, Z., Huang, J., ... Zhang, F. (2014b). Producing more grain with lower environmental costs. *Nature*, 514(7523), 486–499. <https://doi.org/10.1038/nature13609>
- Davey, J. W., Hohenlohe, P. A., Etter, P. D., Boone, J. Q., Catchen, J. M., & Blaxter, M. L. (2011). Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nature Reviews Genetics*, 12(7), 499–510. <https://doi.org/10.1038/nrg3012>
- Dayton, L. (2014). Blue-sky rice. *Nature*, 514, S52–S54. <https://doi.org/10.1038/514S52a>
- Dingkuhn, M., Luquet, D., Fabre, D., Muller, B., Yin, X., & Paul, M. J. (2020). The case for improving crop carbon sink strength or plasticity for a CO₂-rich future. *Current Opinion in Plant Biology*, 56, 259–272. <https://doi.org/10.1016/j.pbi.2020.05.012>
- Donald, C. M. (1968). Breeding of crop ideotypes. *Euphytica*, 17, 385–403. <https://doi.org/10.1007/BF00056241>
- Driever, S. M., Lawson, T., Andralojc, P. J., Raines, C. A., & Parry, M. A. J. (2014). Natural variation in photosynthetic capacity, growth, and yield in 64 field-grown wheat genotypes. *Journal of Experimental Botany*, 65, 4959–4973. <https://doi.org/10.1093/jxb/eru253>
- Ebana, K., Yonemaru, J. I., Fukuoka, S., Iwata, H., Kanamori, H., Namiki, N., Nagasaki, H., & Yano, M. (2010). Genetic structure revealed by a whole-genome single-nucleotide polymorphism survey of diverse accessions of cultivated Asian rice (*Oryza sativa* L.). *Breeding Science*, 60(4), 390–397. <https://doi.org/10.1270/jsbbs.60.390>
- Eble, G. J. (2004). The macroevolution of phenotypic integration. In M. Pigliucci, & K. Preston (Eds.), *Phenotypic integration:*

- Studying the ecology and evolution of complex phenotypes (pp. 253–273). Oxford University Press.
- Erenstein, O. (2012). Resource scarcity gradients and agricultural technologies: Scoping implications in the post-green revolution Indo-Gangetic Plains. *Outlook Agriculture*, 41, 87–95. <https://doi.org/10.5367/oa.2012.0083>
- Fatokun, C., Girma, G., Abberton, M., Gedil, M., Unachukwu, N., Oyatomi, O., Yusuf, M., Rabbi, I., & Boukar, O. (2018). Genetic diversity and population structure of a mini-core subset from the world cowpea (*Vigna unguiculata* (L.) Walp.) germplasm collection. *Scientific Reports*, 8, 1–10. <https://doi.org/10.1038/s41598-018-34555-9>
- Ford-Lloyd, B. V., Newbury, H. J., Jackson, M. T., & Virk, P. S. (2001). Genetic basis for co-adaptive gene complexes in rice (*Oryza sativa* L.) landraces. *Heredity*, 87, 530–536. <https://doi.org/10.1046/j.1365-2540.2001.00937.x>
- Fukagawa, N. K., & Ziska, L. H. (2019). Rice: Importance for global nutrition. *Journal of Nutritional Science and Vitaminology*, 65, S2–S3. <https://doi.org/10.3177/jnsv.65.S2>
- Furbank, R. T., Jimenez-Berni, J. A., George-Jaeggli, B., Potgieter, A. B., & Deery, D. M. (2019). Field crop phenomics: Enabling breeding for radiation use efficiency and biomass in cereal crops. *New Phytologist*, 223, 1714–1727. <https://doi.org/10.1111/nph.15817>
- Garris, A. J., Tai, T. H., Coburn, J., Kresovich, S., & McCouch, S. (2005). Genetic structure and diversity in *Oryza sativa* L. *Genetics*, 169(3), 1631–1638. <https://doi.org/10.1534/genetics.104.035642>
- Gruber, K. (2017). Agro biodiversity: The living library. *Nature*, 544, S8–S10. <https://doi.org/10.1038/544S8a>
- Gutaker, R. M., Groen, S. C., Bellis, E. S., Choi, J. Y., Pires, I. S., Bocinsky, R. K., Slayton, E. R., Wilkins, O., Castillo, C. C., Negrao, S., Oliveira, M. M., Fuller, D. Q., d'Alpoim Guedes, J. A., Lasky, J. R., & Purugganan, M. D. (2020). Genomic history and ecology of the geographic spread of rice. *Nature Plants*, 6(5), 492–502. <https://doi.org/10.1038/s41477-020-0659-6>
- Houle, D., Govindaraju, D., & Omholt, S. (2010). Phenomics: The next challenge. *Nature Reviews Genetics*, 11, 855–866. <https://doi.org/10.1038/nrg2897>
- Hubbart, S., Peng, S., Horton, P., Chen, Y., & Murchie, E. H. (2007). Trends in leaf photosynthesis in historical rice varieties developed in the Philippines since 1966. *Journal of Experimental Botany*, 58(12), 3429–3438. <https://doi.org/10.1093/jxb/erm192>
- Huggins, T. D., Chen, M. H., Fjellstrom, R. G., Jackson, A. K., McClung, A. M., & Edwards, J. D. (2019). Association analysis of three diverse rice (*Oryza sativa* L.) germplasm collections for loci regulating grain quality traits. *Plant Genome*, 12(1), 170085. <https://doi.org/10.3835/plantgenome2017.09.0085>
- Ikeda, M., Hirose, Y., Takashi, T., Shibata, Y., Yamamura, T., Komura, T., Doi, K., Ashikari, M., Matsuoka, M., & Kitano, H. (2010). Analysis of rice panicle traits and detection of QTLs using an image analyzing method. *Breeding Science*, 60(1), 55–64. <https://doi.org/10.1270/jsbbs.60.55>
- Jiang, Y., Qian, H., Wang, L., Feng, J., Huang, S., Hungate, B. A., van Kessel, C., Horwath, W. R., Zhang, X., Qin, X., Li, Y., Feng, X., Zhang, J., Deng, A., Zheng, C., Song, Z., Hu, S., van Groenigen, K. J., & Zhang, W. (2018). Limited potential of harvest index improvement to reduce methane emissions from rice paddies. *Global Change Biology*, 25(2), 686–698. <https://doi.org/10.1111/gcb.14529>
- Jin, L., Lu, Y., Xiao, P., Sun, M., Corke, H., & Bao, J. (2010). Genetic diversity and population structure of a diverse set of rice germplasm for association mapping. *Theoretical and Applied Genetics*, 121(3), 475–487. <https://doi.org/10.1007/s00122-010-1324-7>
- Jones, M. B., Finnan, J., & Hodkinson, T. R. (2015). Morphological and physiological traits for higher biomass production in perennial rhizomatous grasses grown on marginal land. *GCB Bioenergy*, 7, 375–385. <https://doi.org/10.1111/gcbb.12203>
- Kadam, N., Struik, P. C., Rebolledo, C., Yin, X., & Jagadish, K. S. V. (2018). Genome wide association provides novel genomic loci controlling grain yield of rice and its component traits under water-deficit stress during the reproductive stage. *Journal of Experimental Botany*, 69(16), 4017–4032. <https://doi.org/10.1093/jxb/ery186>
- Kadam, N. N., Tamilselvan, A., Lawas, L. M. F., Quinones, C., Bahuguna, R. N., Thomson, M. J., Dingkuhn, M., Muthurajan, R., Struik, P. C., Yin, X., & Jagadish, S. V. K. (2017). Genetic control of plasticity in root morphology and anatomy of rice in response to water-deficit. *Plant Physiology*, 174(4), 2302–2315. <https://doi.org/10.1104/pp.17.0050>
- Khush, G. S. (2001). Green revolution: The way forward. *Nature Reviews Genetics*, 2(10), 815–822. <https://doi.org/10.1038/35093585>
- Koch, K. (2004). Sucrose metabolism: Regulatory mechanisms and pivotal roles in sugar sensing and plant development. *Current Opinion in Plant Biology*, 7, 235–246. <https://doi.org/10.1016/j.pbi.2004.03.014>
- Kumari, S., Singh, P., Singla-Pareek, S. L., & Pareek, A. (2009). Heterologous expression of a salinity and developmentally regulated rice cyclophilin gene (*OsCyp2*) in *E. coli* and *S. cerevisiae* confers tolerance towards multiple abiotic stresses. *Molecular Biotechnology*, 42(2), 195–204. <https://doi.org/10.1007/s12033-009-9153-0>
- Lubis, I., Shiraiwa, T., Ohnishi, M., Horige, T., & Inoue, N. (2003). Contribution of sink and source sizes to yield variation among rice cultivars. *Plant Production Science*, 6, 119–125. <https://doi.org/10.1626/pp.6.119>
- Mascher, M., Schreiber, M., Scholz, U., Graner, A., Reif, J. C., & Stein, N. (2019). Genebank genomics bridges the gap between the conservation of crop diversity and plant breeding. *Nature Genetics*, 51(7), 1076–1081. <https://doi.org/10.1038/s41588-019-0443-6>
- Mooney, B. P. (2009). The second green revolution? Production of plant-based biodegradable plastics. *Biochemical Journal*, 418(2), 219–232. <https://doi.org/10.1042/BJ20081769>
- Mora-Ramirez, I., Weichert, H., von Wiren, N., Froberg, C., de Bodt, S., Schmidt, R. C., & Weber, H. (2021). The da1 mutation in wheat increases grain size under ambient and elevated CO2 but not grain yield due to trade-off between grain size and grain number. *Plant-Environment Interactions*, 2, 61–73. <https://doi.org/10.1002/pei3.10041>
- Palme, K., Li, X., & Teale, W. D. (2014). Towards second green revolution: Engineering nitrogen use efficiency. *Journal of Genetics and Genomics*, 41(6), 315–316. <https://doi.org/10.1016/j.jgg.2014.05.003>
- Pareek, A., Dhankher, O. P., & Foyer, C. H. (2020). Mitigating the impact of climate change on plant productivity and ecosystem sustainability. *Journal of Experimental Botany*, 71(2), 451–456. <https://doi.org/10.1093/jxb/erz518>

- Peng, S., Laza, R. C., Visperas, R. M., Sanico, A. L., Cassman, K. G., & Kush, G. S. (2001). Grain yield of rice cultivars and lines developed in the Philippines since 1966. *Crop Sciences*, 40(2), 307–314. <https://doi.org/10.2135/cropsci2000.402307x>
- Qian, Q., Guo, L. B., Smith, S. M., & Li, J. Y. (2016). Breeding high-yield superior quality hybrid super rice by rational design. *National Science Review*, 3, 283–294. <https://doi.org/10.1093/nsr/nww006>
- Qu, M., Zheng, G., Hamdani, S., Essemine, J., Song, Q., Wang, H., Chu, C., Sirault, X., & Zhu, X. G. (2017). Leaf photosynthetic parameters related to biomass accumulation in a global rice diversity survey. *Plant Physiology*, 175(1), 248–258. <https://doi.org/10.1104/pp.17.00332>
- Rashid, K. A., Kahliq, I., Farooq, M. O., & Ahsan, M. Z. (2014). Correlation and cluster analysis of some yield and yield-related traits in Rice (*Oryza sativa*). *International Journal of Advance Agricultural Research*, 2, 290–295.
- Ray, D. K., Ramankutty, N., Mueller, N. D., West, P. C., & Foley, J. A. (2012). Recent patterns of crop yield growth and stagnation. *Nature Communications*, 3, 1–7. <https://doi.org/10.1038/ncomms2296>
- Ricklefs, R. E. (2004). Cladogenesis and morphological diversification in passerine birds. *Nature*, 430(6997), 338–341. <https://doi.org/10.1038/nature02700>
- Ricklefs, R. E. (2006). Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, 87, S3–S13. [https://doi.org/10.1890/0012-9658\(2006\)87\[3:EDATO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[3:EDATO]2.0.CO;2)
- Rohila, J. S., Edwards, J. D., Tran, G. D., Jackson, A. K., & McClung, A. M. (2019). Identification of superior alleles for seedling stage salt tolerance in the USDA rice mini-core collection. *Plants*, 8(11), 472. <https://doi.org/10.3390/plants8110472>
- Roos, E., Bajzelj, B., Smith, P., Patel, M., Little, D., & Garnett, T. (2017). Greedy or needy? Land use and climate impacts of food in 2050 under different livestock futures. *Global Environmental Change*, 47, 1–12. <https://doi.org/10.1016/j.gloenvcha.2017.09.001>
- Seck, P. A., Diagne, A., Mohanty, S., & Wopereis, M. C. (2012). Crops that feed the world 7: Rice. *Food Security*, 4, 7–24. <https://doi.org/10.1007/s12571-012-0168-1>
- Sinclair, T. R. (1998). Historical changes in harvest index and crop nitrogen accumulation. *Crop Science*, 38(3), 638–643. <https://doi.org/10.2135/cropsci1998.0011183X003800030002x>
- Smith, M. R., Rao, I. M., & Merchant, A. (2018). Source-sink relationships in crop plants and their influence on yield development and nutritional quality. *Frontiers in Plant Sciences*, 20(9), 1889. <https://doi.org/10.3389/fpls.2018.01889>
- Spindel, J. E., Begum, H., Akdemir, D., Collard, B., Redona, E., Jannink, J. L., & McCouch, S. (2016). Genome-wide prediction models that incorporate de novo GWAS are a powerful new tool for tropical rice improvement. *Heredity*, 116, 395–408. <https://doi.org/10.1038/hdy.2015.113>
- Tan, Y., Sun, L., Song, Q., Mao, D., Zhou, J., Jiang, Y., Wang, J., Fan, T., Zhu, Q., Huang, D., Xiao, H., & Chen, C. (2020). Genetic architecture of subspecies divergence in trace mineral accumulation and elemental correlations in the rice grain. *Theoretical and Applied Genetics*, 133, 529–545. <https://doi.org/10.1007/s00122-019-03485-z>
- Tanaka, A., Diagne, M., & Saito, K. (2015). Causes of yield stagnation in irrigated lowland rice systems in the Senegal River Valley: Application of dichotomous decision tree analysis. *Field Crops Research*, 176, 99–107. <https://doi.org/10.1016/j.fcr.2015.02.020>
- Teichmann, T., & Muhr, M. (2015). Shaping plant architecture. *Frontiers in Plant Sciences*, 9(6), 233. <https://doi.org/10.3389/fpls.2015.00233>
- Tuhina-Khatun, M., Hanafi, M. M., RafiiYusop, M., Wong, M. Y., Salleh, F. M., & Ferdous, J. (2015). Genetic variation, heritability, and diversity analysis of upland rice (*Oryza sativa* L.) genotypes based on quantitative traits. *BioMed Research International*, 1, 290861. <https://doi.org/10.1155/2015/290861>
- Upadhyaya, H. D., & Ortiz, R. (2001). A mini core subset for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. *Theoretical and Applied Genetics*, 102, 1292–1298. <https://doi.org/10.1007/s00122-001-0556-y>
- Vaughan, D. A., Lu, B. R., & Tomooka, N. (2008). The evolving story of rice evolution. *Plant Science*, 174(4), 394–408. <https://doi.org/10.1016/j.plantsci.2008.01.016>
- Wang, C. H., Zheng, X. M., Xu, Q., Yuan, X. P., Huang, L., Zhou, H. F., Wei, X. H., & Ge, S. (2014). Genetic diversity and classification of *Oryza sativa* with emphasis on Chinese rice germplasm. *Heredity*, 112, 489–496. <https://doi.org/10.1038/hdy.2013.130>
- Wang, W., Mauleon, R., Hu, Z., Chebotarov, D., Tai, S., Wu, Z., Li, M., Zheng, T., Fuentes, R. R., Zhang, F., Mansueto, L., Copetti, D., Sanciangco, M., Palis, K. C., Xu, J., Sun, C., Fu, B., Zhang, H., Gao, Y., ... Leung, H. (2018). Genomic variation in 3,010 diverse accessions of Asian cultivated rice. *Nature*, 557, 43–49. <https://doi.org/10.1038/s41586-018-0063-9>
- Wassmann, R., Jagadish, S. V. K., Sumfleth, K., Pathak, H., Howell, G., Ismail, A., Serraj, R., Redona, E., Singh, R. K., & Heuer, S. (2009). Regional vulnerability of climate change impacts on Asian rice production and scope for adaptation. *Advances in Agronomy*, 102, 91–133. [https://doi.org/10.1016/S0065-2113\(09\)01003-7](https://doi.org/10.1016/S0065-2113(09)01003-7)
- Xu, L., Yuan, K., Yuan, M., Meng, X., Chen, M., Wu, J., Li, J., & Qi, Y. (2020). Regulation of rice tillering by RNA-Directed DNA Methylation at miniature inverted-repeat transposable elements. *Molecular Plant*, 13(6), 851–863. <https://doi.org/10.1016/j.molp.2020.02.009>
- Yang, H., Li, J., Yang, J., Wang, H., Zou, J., & He, J. (2014). Effects of nitrogen application rate and leaf age on the distribution pattern of leaf SPAD readings in the rice canopy. *PLoS One*, 9(2), e88421. <https://doi.org/10.1371/journal.pone.0088421>
- Zhang, D. Y., Sun, G. J., & Jiang, X. H. (1999). Donald's ideotype and growth redundancy: A game theoretical analysis. *Field Crops Research*, 61, 179–187. <https://doi.org/10.1371/journal.pone.0070006>
- Zhang, M., Pinson, S. R., Tarpley, L., Huang, X. Y., Lahner, B., Yakubova, E., Baxter, I., Guerinot, M. L., & Salt, D. E. (2014). Mapping and validation of quantitative trait loci associated with concentrations of 16 elements in unmilled rice grain. *Theoretical and Applied Genetics*, 127, 137–165. <https://doi.org/10.1007/s00122-013-2207-5>
- Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D. B., Huang, Y., Huang, M., Yao, Y., Bassu, S., Ciais, P., Durand, J. L., Elliott, J., Ewert, F., Janssens, I. A., Li, T., Lin, E., Liu, Q., Martre, P., Müller, C., ... Asseng, S. (2017). Temperature increase reduces global yields of major crops in four independent estimates. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 9326–9331. <https://doi.org/10.1073/pnas.1701762114>

- Zhu, X. G., Long, S. P., & Ort, D. R. (2010). Improving photosynthetic efficiency for greater yield. *Annual Review of Plant Biology*, 61, 235–261. <https://doi.org/10.1146/annurev-arplant-042809-112206>
- Ziska, L. H., Gealy, D. R., Tomecek, M. B., Jackson, A. K., & Black, H. L. (2012). Recent and projected increases in atmospheric CO₂ concentrations can enhance gene flow between wild and genetically altered rice (*Oryza sativa*). *PLoS One*, 7, e37522. <https://doi.org/10.1371/journal.pone.0037522>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Anwar, K., Joshi, R., Morales, A., Das, G., Yin, X., Anten, N. P. R., Raghuvanshi, S., Bahuguna, R. N., Singh, M. P., Singh, R. K., van Zanten, M., Sasidharan, R., Singla-Pareek, S. L., & Pareek, A. (2022). Genetic diversity reveals synergistic interaction between yield components could improve the sink size and yield in rice. *Food and Energy Security*, 11: e334. <https://doi.org/10.1002/fes3.334>