More and more of less and less: Is genomics-based breeding of dry direct-seeded rice (DDSR) varieties the need of hour?

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Summary
Rice is a staple food for half of the world's population. Changing climatic conditions, water and labour scarcity are the major challenges that shall limit future rice production. Dry direct-seeded rice (DDSR) is emerging as an efficient, resources conserving, mechanized, climate smart and economically viable strategy to be adopted as an alternative to puddled transplanted rice (TPR) with the potential to address the problem of labour-water shortages and ensure sustainable rice cultivation. Despite these benefits, several constraints obstruct the adoption of DDSR. In principle, the plant type for DDSR should be different from one for TPR, which could be achieved by developing rice varieties that combine the traits of upland and lowland varieties. In this context, recent advances in precise phenotyping and NGS-based trait mapping led to identification of promising donors and QTLs/generes for DDSR favourable traits to be employed in genomic breeding. This review discusses the important traits influencing DDSR, research studies to clarify the need for breeding DDSR-specific varieties to achieve enhanced grain yield, climate resilience and nutrition demand. We anticipate that in the coming years, genomic breeding for developing DDSR-specific varieties would be a regular practice and might be further strengthened by combining superior haplotypes regulating important DDSR traits by haplotype-based breeding.

Introduction
Rice is cultivated in the four different ecosystems (irrigated, rainfed upland, rainfed lowland and flood-prone deep water). However, the decline of water and labour availability, energy scarcity, increasing input costs and climatic change threatens sustainability of rice cultivation under puddled transplanted ecologies (Mahajan et al., 2011). To develop an alternate method of rice cultivation without compromising crop productivity and to achieve economic security is indeed a great challenge. In this context, direct-seeded rice (DSR) technologies have the potential to effectively address the problem of water and labour scarcity in both irrigated and rainfed areas (Liu et al., 2015).

The DSR cultivation system is classified as dry-DSR, wet-DSR and water-DSR. Traditionally, the DSR method has been practiced in rainfed upland and rainfed shallow lowland areas of Asia and is popular in irrigated areas where water is limited (Kumar and Ladha, 2011). In dry-DSR (DDSR), seeds are sown into the soil which is not puddled but may be either zero-tier (ZT-DDSR) or dry till conventional tillage (CT-DDSR). In wet-DSR and water-DSR, pre-germinated seeds are sown into puddled soil and standing water, respectively. Wet-DSR or mechanical transplanting without changing tillage practices should be opted in the areas where water is available, but labour scarcity persists. The areas, where both labour and water are limited, adopting DDSR either with dry or zero or reduced tillage are more feasible (Rao et al., 2017). Dry direct seeding method has been adopted in aerobic rice and upland rice (Kumar and Ladha, 2011). Taking advantage of saving scarce resources and increasing productivity, DDSR is considered as a promising option for rice production (Chauhan et al., 2017; Jabran et al., 2017).

Currently, the rice varieties breed for TPR (transplanted puddled rice) are being used in the DDSR system; these varieties do not fit completely and fail to achieve their potential yield under DDSR (Mahajan et al., 2018). Although this approach is straightforward, it suffers from few limitations, and in this context, it is evident that specific breeding efforts are essential to develop DDSR-suited varieties which perform best under these constraints without any compromise on grain yield. The unavailability of suitable varieties and lack of proper understanding about DDSR...
suitable traits that could enhance rice yield and adaptability under direct-seeded condition are major hurdles in DDSR to successfully replace TPR (Sandhu et al., 2015).

Though DDSR has several advantages over TPR, there are some constraints in its adoption that need to be addressed (Figure 1). The DDSR suitable plant type can be achieved by developing rice varieties through combining traits of upland varieties (tolerance of water deficit, early vigour and weed competitiveness) and lowland varieties (high yield potential, efficient nutrient uptake and good grain quality). The genomic-breeding efforts to develop varieties possessing traits needed for higher yield potential in DDSR are underway (Sandhu et al., 2019b). The development of DDSR varieties with ideal plant type could be a sustainable strategy to cope up with water-labour scarcity and climate change. As a preliminary step, we have performed comprehensive analysis on the correlation among major traits including yield attributing traits, grain nutrition and stress tolerance, to conclude whether specific breeding efforts and varieties are required for the DDSR system.

The need for developing rice varieties suiting DDSR

To understand whether there is a need to adapt specific breeding strategies to develop rice varieties for DDSR, we analysed the correlation of the major traits including yield, nutrition (grain Fe and Zn content), abiotic (Fe deficiency tolerance) and biotic (bacterial leaf blight) stress between TPR and DDSR conditions. These studies were conducted under DDSR breeding programme at the International Rice Research Institute-South Asia Hub (IRRI-SAHI), Hyderabad, using different subsets of 3K panel and mapping populations (Source data are unpublished). The Pearson correlation coefficient was used for analysing the relationship between various DDSR traits at a statistical significance of $P < 0.05$. This was performed using the ‘corrplot’ package in R (R.3.6.1).

Comparison of yield and yield-related traits

An experimental study was conducted during the year 2016 and 2018 to understand the relationship between yield and related traits under DDSR and TPR situations. A subset of 350 lines from the 3K panel was sown/planted under both DDSR and TPR situations with a complete package of practices from sowing to harvesting for ideal crop establishment. Phenotypic data under DDSR and TPR were recorded for days to 50% flowering (DFF), panicle length (PL), number of tillers (NT), plant height (PH) and grain yield (GY). We observed a highly significant positive association for DFF between DDSR and TPR. Other traits like NT, PL and PH showed a positive non-

Figure 1 Benefits and constraints associated with dry direct-seeded rice (DDSR). DDSR system has various advantages over the transplanted system such as reduced water usage, reduced methane emissions, compatible with mechanization, less labour requirement and shorter crop duration. At the same time, several challenges that have to be addressed to make DDSR a regular practice including, susceptibility to diseases and soil-borne pathogens, weed rivalry, micronutrient deficiencies, lodging susceptibility, etc. [Colour figure can be viewed at wileyonlinelibrary.com]
significant association, whereas GY showed negative non-significant association between DDSR and TPR (Figure 2a). These results suggest that direct usage of TPR varieties under DDSR system might not be an ideal option in the long run and there is a compelling need to identify potential candidate QTLS/genes/haplotypes and deploy them in specific breeding programmes in order to develop high-yielding DDSR-suited varieties.

Comparison of grain nutritional traits

The uptake of zinc (Zn) and iron (Fe) in grain is influenced by genotypic or environment factors such as soil texture, soil moisture, availability of nutrients in soil (content and its form), abiotic stresses and agronomic practices (Macedo, 2012). To understand the differences in the accumulation of Zn and Fe in rice grain under DDSR and TPR conditions, an experiment was conducted during 2017 and 2018 with 128 accessions of 3K panel subset. Estimation of grain Zn and Fe content was done with X-ray fluorescence. The Zn content of the accessions was ranged from 17.1 to 46.5 ppm and 11.3 to 26.3 ppm under TPR and DDSR, respectively, whereas Fe content was ranged from 11.5 to 18.5 ppm and 7.6 to 19.8 ppm under TPR and DDSR, respectively. Under TPR condition, the $O_2$ released by roots cause oxidation of Fe, which further reduces rhizosphere pH and limits the release of Zn from highly insoluble fractions (Gao et al., 2006). In DDSR, the aerobic dry condition often accelerates organic matter oxidation, restricting Zn availability in soil (Rehman et al., 2012). The aerobic condition also causes oxidation of available ferrous ($Fe^{2+}$) to unavailable ferric ($Fe^{3+}$) form in the soil (Joshi et al., 2013). Therefore, shift from TPR to DDSR sets a problem of soil Zn and Fe deficiency (Xue et al., 2016). In the current study, correlation analysis showed a significant association for grain Zn content under TPR and DDSR but no such association was observed for Fe content (Figure 2b). This implies the need for specific breeding efforts for enhancing grain Fe content under the DDSR system.

Figure 2 Understanding the correlation of major traits between dry direct-seeded rice (DDSR) and transplanted rice (TPR) system. Plots of Pearson’s $R$-values showing correlation between DDSR and TPR for (a) yield and yield-contributing traits – a highly significant and positive association for DFF is observed between TPR and DDSR; however, traits like panicle length (PL), number of tillers (NT) and plant height (PH) show positive non-significant association whereas grain yield (GY) shows negative non-significant association between TPR and DDSR, (b) grain Fe and Zn concentration – a significant association for Zn between TPR and DDSR condition is observed but no such association for Fe is observed, (c) for Fe deficiency tolerance – a non-significant correlation for leaf chlorosis and plant yield under TPR and DDSR situations is observed indicating the necessity of breeding efforts specific to DDSR conditions to address soil Fe deficiency, (d) for BLB disease – there is no difference in BLB disease severity in TPR and DDSR condition. (DDSR: Dry direct-seeded rice, TPR: transplanted rice, GY: grain yield (kg/ha), PH: plant height (cm), PL: panicle length (cm), NT: number of tillers, DFF: days to 50% flowering, Fe: grain iron content (ppm), Zn: grain Zn content (ppm), SPY: single plant yield (g), IDC: iron deficiency chlorosis, BLB: Bacterial leaf blight). *significant at <0.05 level, **significant at <0.01 level, *** significant at <0.001 level, blank for non-significant. [Colour figure can be viewed at wileyonlinelibrary.com]
Comparison of micronutrient deficiency traits

The soil micronutrient deficiency especially for Fe and Zn in rice is an important concern affecting crop yield and quality traits. Under aerobic condition, oxidation of available ferrous (Fe$^{2+}$) to unavailable ferric (Fe$^{3+}$) form leads to iron deficiency in rice (Joshi et al., 2013). By understanding the genetic and physiological mechanism for micronutrient deficiency tolerance, the available genetic variability can be utilized more efficiently in breeding programmes for developing micronutrient efficient rice varieties. Besides, there is an imperative to understand the mineral deficiency response and whether the same or different genomic regions regulate the response to these deficiencies under TPR and DDSR system. In this context, an experiment was conducted during 2018 to study the Fe deficiency tolerance and its correlations with yield in BC$_1$F$_2$ progenies of mapping population derived from Naveen (Fe deficiency susceptible parent) × Basmati 370 (Fe deficiency-tolerant parent) cross. The Fe deficiency chlorosis (IDC) scoring was carried out at tillering stage using 1-9 scale as described by Hoan et al. (1992). The IDC and plant yield under DDSR and TPR showed no correlation (Figure 2c) that might be due to different regulatory mechanisms, which indicates the necessity of breeding efforts specific to DDSR conditions to address soil iron deficiency.

Comparison of response to bacterial leaf blight (BLB)

BLB is one of the serious threats to rice production, and there are no comprehensive studies on its comparative severity between DDSR and TPR. During 2018, a study was conducted to compare the BLB disease severity and their correlation under DDSR and TPR conditions using a subset 3K-RG panel consisting of 75 lines. A highly virulent isolate of Xanthomonas oryzae pv. oryzae (Xoo) IX-020 collected from Indian Institute of Rice Research (II RR), Hyderabad (India), was used for BLB screening. Top five leaves of three random plants of each entry were clip inoculated at maximum tillering stage. The disease assessment was done 14 days after inoculation by measuring the lesion length in centimetres. Average lesion length of each entry was used to study the correlation between DDSR and TPR. The correlation analysis revealed that the disease severity was positively correlated in DDSR and TPR (Figure 2d). Correlation was highest between DDSR and TPR ($R = 0.94$) ($P < 0.05$). Therefore, from the study, we conclude that there will not be much difference in BLB disease severity in TPR and DDSR condition. Thus, the identified BLB resistant genes under TPR conditions are expected to perform well under DDSR.

Traits for developing DDSR varieties

The poor understanding of favourable traits is one of the major limitations in achieving adaptability and yield potential under DDSR. Information of DDSR suitable traits can help us to adapt DDSR by combining novel genomic techniques in varietal development with advances in the mechanization of DDSR. Genomic research advances in the recent past have led to the identification of QTLs, donors and genes for several traits likely to be important for DDSR condition (Table 1, Figure 3).

Anaerobic germination and tolerance to early submergence

DDSR is mainly grown during the monsoon season, and thus, heavy rains immediately after sowing create a submergence situation leading to poor emergence. Anaerobic germination is an important trait for establishing a good crop and is one of the possible reasons for the success of DDSR (Septiningsih et al., 2013). A total of 8000 GeneBank accessions and breeding lines were screened for tolerance to anaerobic germination at IRRI, and Kho An On (Oryza sativa L. subsp. japonica) was reported as a highly tolerant genotype (Angaji et al., 2010). A large number of QTLs with significant effects on anaerobic germination were identified (Angaji et al., 2010; Baltazar et al., 2014; Ghosal et al., 2019; Septiningsih et al., 2013). QTL, qAGS$_{9.2}$ (chromosome 9), was fine mapped to OsTPP7 that mobilizes starch to promote embryo germination and coleoptile elongation (Kretzschmar et al., 2015). Recently, a major effect QTL, qSUR$_{7.7}$, for survival under anaerobic condition (SUR) reported by Ghosal et al. (2019), showed tight linkage with the Rc gene which codes for pericarp colour. Exploration of prominent QTLs for AG tolerance during germination may provide robust targets to accelerate marker-assisted breeding (MAB) for developing DDSR suitable varieties.

Early uniform emergence

Early uniform emergence (EUE) and seedling development are the critical determinants of crop establishment and subsequent yield. The EUE develops a deep root system which helps in acclimatization of the emerged seedlings before the upper soil layer gets dry. The EUE is contributed by various traits viz. early germination, high germination rate and more seedling vigour. Two major and consistent QTLs, qEMM$_{1.1}$, (chromosome 1) and qEMM$_{1.1}$, (chromosome 11), for early uniform emergence contributed by Moroberekan were reported by Dixit et al. (2015) from BC$_2$F$_3$ (Moroberekan/Swarna) population. Recently, Singh et al. (2017) reported a major effect QTL, qEUE$_{3.2}$, (chromosome 3), using BC$_2$F$_3$ (Moroberekan/Swarna) population. Several QTLs for EUE and associated traits have been reported to be pyramided along with yield traits (Sandhu et al., 2015; Singh et al., 2017).

Early vigour

Early vigour/biomass accumulation during the early vegetative stage is one of the important traits for adaptation of rice to direct seeding (Sandhu et al., 2015). Early vigour (EV) is defined by rapid germination (germination rate, germination percentage and germination index), seedling height, mesocotyl and shoot length, root length, etc. The most stable QTL across genetic backgrounds for early vigour, qEVS$_{9.1}$, (chromosome 9), co-located with grain yield QTL qGY$_{9.1}$, was reported (Sandhu et al., 2015). Two QTL hot spots on chromosomes 3 ($qEV3.1$, $qEV5.1$, $qSHL3.1$, $qSL3.1$, $qSFWS3.1$, $qTFW3.1$, $qQDWS3.1$) and 5 ($qEV5.1$, $qEUE5.1$, $qSHL5.1$, $qSL5.1$, $qSFWS5.1$, $qQDWS5.1$, $qQDWS5.1$) for early vigour, early uniform emergence, shoot length, stem length, shoot fresh weight, shoot dry weight, total fresh weight, total dry weight and root dry weight traits have been recently identified by Singh et al. (2017). Exploration of clustered QTLs can lead to breed superior DDSR-suited varieties.

Competitiveness against weeds

During the early vegetative stage, the crop size difference between rice and weed is small, which reduces crop competitiveness under the DDSR situation. The early vigour and associated traits can promote crop competitiveness against weeds (Okami et al., 2011). A highly significant QTL, qSH$_{1.1}$, (chromosome 1), for crop competitiveness is recently reported (Ghosal et al., 2019). The potential of using early flooding to wash out initial weeds is limited in rice (Rao et al., 2017) and can be
Table 1 Favourable traits, QTLs/genes for developing DDSR varieties

| Trait                              | QTL/Gene | Donor                        | Chromosome | Reference                                      |
|------------------------------------|----------|------------------------------|------------|-----------------------------------------------|
| Early uniform emergence            | qEMM11.1 | IR91648-B-32-B               | 11         | Dixit et al. (2015)                           |
| Early vigour                       | qEVV9.1  | IR94226-B-177-B              | 9          | Sandhu et al. (2015)                          |
| Grain yield under water deficit    | qGY9.1   | IR94225-B-82-B, IR94226-B-177-B | 8          | Sandhu et al. (2013)                          |
|                                     | qGY9.1   | IR94225-B-82-B               | 6          | Sandhu et al. (2015)                          |
|                                     | qGY10.1  | IR94225-B-82-B               | 9          | Sandhu et al. (2015)                          |
|                                     | qGY11.1  | IR94225-B-82-B               | 10         | Sandhu et al. (2015)                          |
| Root length                         | qRL8.2   | IR94225-B-82-B, IR94226-B-177-B | 8          | Sandhu et al. (2013)                          |
| Root hair length                   | qRHL1.1  | IR94225-B-82-B, IR94226-B-177-B | 1          | Sandhu et al. (2013)                          |
| Root hair density                  | qRHD1.1  | IR94225-B-82-B, IR94226-B-177-B | 5          | Sandhu et al. (2013)                          |
| Nodal root number                  | qNR5.1   | IR94225-B-82-B, IR94226-B-177-B | 5          | Sandhu et al. (2013)                          |
| Nutrient uptake                    | qNU5.1   | IR94225-B-82-B               | 5          | Sandhu et al. (2013)                          |
| Anaerobic germination              | qAGS5.2  | IR93312-30-101-20-3-66-6     | 9          | Angaji et al. (2010)                          |
| Lodging resistance                 | qLDSG5.2 | IR91648-B289-B               | 3          | Dixit et al. (2015)                           |
|                                     | qCD1.1   | IR94225-B-82-B               | 1          | Yadav et al. (2017)                           |
| Drought tolerance                  | qDTY1.1  | IR94225-B-82-B               | 1          | Bernier et al. (2007), Venuprasad et al. (2009), Vikram et al. (2011), Ghimire et al. (2012), Swamy et al. (2013), Dixit et al. (2012) |
|                                     | qDTY2.1  | IR94225-B-82-B               | 2          | Ye et al. (2012, 2015)                        |
|                                     | qDTY2.2  | IR94225-B-82-B               | 3          | Dixit et al. (2015)                           |
|                                     | qDTY4.1  | IR94225-B-82-B               | 4          | Dixit et al. (2015)                           |
|                                     | qDTY6.1  | IR94225-B-82-B               | 5          | Dixit et al. (2015)                           |
|                                     | qDTY12.1 | IR94225-B-82-B               | 6          | Dixit et al. (2015)                           |
| Heat tolerance                     | qHTSF4.1 | N22                          | 4          | Jagadish et al. (2010), Ye et al. (2012, 2015) |
| Cold tolerance                     | qPSST-3  | Geumobyeo                    | 3          | Suh et al. (2010)                             |
|                                     | qPSST-7  | IR94225-B-82-B               | 7          | Suh et al. (2010)                             |
| Nematode resistance/tolerance      | qYR5.1   | R78877-208-B-1-2             | 5          | Galeng-Lawilao et al. (2018)                  |
| Brown spot resistance              | qBS9     | Tadukan                      | 9          | Sato et al. (2008, 2015)                      |
| Gall midge resistance              | Gm4      | Abhaya                       | 12         | Sama et al. (2012)                            |
| Blast resistance                   | P9       | IRBL9                        | 6          | Qu et al. (2006)                              |
| Bacterial blight resistance        | Xa4      | IRBB60                       | 11         | Loan et al. (2006)                            |
| BPH resistance                     | Bph3     | Rathu heenati                | 6          | Jairin et al. (2007)                          |
|                                     | Bph17    | IR65482-7-216-1-2            | 4          | Bhasin et al. (2012)                          |
|                                     | Bph18    | IRGC105710                   | 7          | Kumar et al. (2012)                           |
|                                     | Bph20    | IRGC1825                     | 4          | Sun et al. (2005)                             |
|                                     | Bph21    | IR71033-121-15               | 4          | Iena et al. (2006)                            |
|                                     |          |                              | 12         | Rahman et al. (2009)                          |
enhanced by introducing QTLs for anaerobic germination (qAG9.2) and tolerance to early submergence (Sub1). Rice morphological characteristics, and root traits for enhanced nutrient uptake, are associated with weed competitiveness (Rao et al., 2017).

Herbicide tolerance

Rice herbicide mutants have already been developed (Table 2), and their performance needs to be assessed under DDSR conditions. A rice gene, HIS1 (HPDD INHIBITOR SENSITIVE 1) encoding oxidase, that confers resistance to benzobicyclon (BBC) and other β-triketone herbicides have been recently identified (Maeda et al., 2019). At HIS1, locus mutations in Os02g0280700 gene (similar to iron/ascorbate-dependent oxidoreductase) play an important role in herbicide tolerance. A 28 base pair deletion in exon IV causes susceptibility, whereas an insertion of the retrotransposon Tos17 within exons I and V of this gene leads to BBC tolerance. Several herbicide-tolerant mutants are reported, and further efforts to identify candidate genes/genomic regions associated with herbicide tolerance help in DDSR breeding programmes.

Nematode resistance/tolerance

Aerobic soil favours occurrence of root-knot nematodes, and nematode infestation is a major bottleneck in DDSR. Rice root-knot nematode, Meloidogyne graminicola, is a predominant nematode species associated with rice under rainfed or aerobic conditions. Lack of resistance to nematodes is a significant factor hindering the genetic improvement of cultivated rice. The O. longistaminata and O. glaberrima were reported to possess natural resistance to M. graminicola, but the attempts failed to introgress resistance from O. glaberrima to O. sativa (Cabasan et al., 2018). From the global rice panel, two Asian rice cultivars, LD24 and Khao Pahl Maw (KPM), were reported as potential resistant sources to M. graminicola (Dimkpa et al., 2015). Three main effect QTLs, qMGR4.1, qMGR7.1 and qMGR9.1, for field resistance to M. graminicola in Asian rice (Galeng-Lawilao et al., 2018) and a resistance locus from 23 Mbp to the bottom of chromosome 11 (Lahari et al., 2019) are reported. Further extensive studies to select potential resistant sources, genes and QTLs can pave the way to overcome yield losses in DDSR caused by M. graminicola infestation.

![Figure 3](image-url) Development of tailored rice varieties suiting DDSR system. Years of efforts in trait development and mapping activities have led to the identification of key traits influencing DSR and their associated genomic regions/QTLs. This includes i. root plasticity and architecture – qNR4.1, qNR5.1 (2.7-20% G), qRL8.2 (19.8-38.8% G), qRHD1.1 (4.1-17.3% G), DRO1, qRHL1.1, qRHD5.1, qRHD8.1; ii. nutrient uptake and use efficiency – qN5.1 (16.2-29.5% G), qP5.2 (16.4-40.7% G), qFe5.2 (10.5-16.3% G); iii. anaerobic germination and tolerance to early submergence – qAG9.1, qAG9.2 (17.9-33.5% G), Sub1; iv. early vigour-related traits – qEVV9.1 (5.7-15.7% G), qEV5.1, qEV5.1; v. early uniform emergence – qEMM1.1 (3.6-7.8% G), qEUE3.1, qEUE3.1; vi. weed competitiveness – qSH1.1 (13.5-34.3% G); vii. herbicide tolerance – HIS1; viii. abiotic stress tolerance – qDTY1.1 (30-36% G), qCTS4a4b, qHTFS4.1; ix. biotic stress tolerance – qYR5.1, qYR11.1 (3.5-4.2% G), qMn4, qMn8, qBph3, qBph17, qBph18, qBph20, qBph21, qPita2, qBS11, qX21, qX33, qX38, qX13, qX5; x. lodging resistance – qLDG3.1, qLDG4.1 (3-6.6% G), qCS1.1, qCD1.1, qCD1.1, SCM2; xi. grain yield under DSR – qGY1.1 (9.1-19.5% G), qGY6.1, qGY6.1, qGY9.1, qGY10.1, qGY11.1, qGY10.1, and qGY10.1; and xii. grain quality – qPGWC6, qCS6, badh2, SSLa, Wx, fgr. (QTLs/gene marked in bold are some of the important targets that need to be quickly deployed in genomic breeding of DDSR varieties, and the range of phenotypic variance explained of each major QTL in different genetic backgrounds (G) and environments (E) is shown under parenthesis). (Colour figure can be viewed at wileyonlinelibrary.com)
Lodging resistance

Lodging resistance is a desirable trait for DDSR as it helps to improve yield, quality of produce and efficiency of mechanical harvesting. Several QTLs for lodging resistant-related traits are reported, viz. prf5, qPRF-8, BSU11, gh2, SCM1, SCM2, SCM3 and SCMA4 (Hu et al., 2008; Kashikwagi et al., 2006, 2016; Okawaka et al., 2010, 2014; Yano et al., 2015). The APO1 gene controlling panicle architecture also enhances culm strength and thickness (Okawaka et al., 2010). Yadav et al. (2017) reported two major effects: QTLs, qCD1.1, and qCS1.1 (chromosome 1) for culm diameter and strength, respectively. A stable QTL (chromosome 2) for the traits contributing to lodging resistance (SM – section modulus and ODMA – outer diameter of the major axis) reported recently by Jiang et al. (2019) was found to possess putative genes responsible for cytokinin signalling, cell cycle signalling, NAC transcription factor signalling and other biological processes. Two QTLs, qCD6 (culm diameter) and qCS6 (culm thickness), incongruent with SCM2/APO1 and qBS2 (bending stress) are reported in the vicinity of SCM4 (Merugumala et al., 2019). The GWAS on a complex mapping population for DDSR traits identified QTLs for culm diameter and stem diameter (chromosome 3) co-located with bc3 and SCM3, respectively (Sandhu et al., 2019a). A significant positive correlation between lodging associated traits and grain yield indicates the major role of lodging resistant traits in improving grain yield under DDSR (Sandhu et al., 2019a; Yadav et al., 2017).

Nutrient uptake

Poor root structure and the inability of roots to cope with the frequent changes in soil structure and conditions obstruct the uptake of water and nutrients under DDSR (Sandhu et al., 2019a). Several genes have been reported for root traits enhancing nutrient efficiency in rice, viz. ELS (N uptake), OsARF12 (Fe uptake) and OsPHR2, OsMYB2P-1, PSTD1 (P uptake) (Dai et al., 2012; Gamuyao et al., 2012; Mochizuki et al., 2014; Qi et al., 2012). Introggression of the major QTL, Pup1 (phosphorus uptake1), led to considerable increase in P acquisition efficiency with higher yield gain (Chin et al., 2011). A major QTL, TOND1 (tolerance of nitrogen deficiency 1), confers tolerance to nitrogen deficiency (Zhang et al., 2015). The QTLs, qALU5,2, qFeU5,2, qZnU5,2, qPU4,1 and qPU5,2 for uptake of Al, Fe, Zn and P, respectively, under aerobic direct-seeded situations were reported by Sandhu et al. (2015). Hartley et al. (2019) reported a key role of OsHTT2.1 (sodium transporter gene) in potassium use efficiency (KUE). The GWAS performed on a complex mapping population revealed co-location of QTL for Fe and P uptake near OsPT9, OsGLK1, nyc3, OsRPK1 and OsCAMA2 genes associated with nutrient uptake, chloroplast development, symbiosis association and stay green phenotype (Sandhu et al., 2019a). A significant and positive correlation between some root traits, water and nutrient uptake and yield under DDSR is reported (Sandhu et al., 2016, 2019a; Suralta et al., 2010).

Grain yield under water-deficit condition

The poor seedling establishment, biotic and abiotic stresses, and weed competition with crop decline the yield in DDSR. Significantly higher grain yield can be obtained in DDSR by enhancing panicle number, grains per panicle, grain weight and lower sterility percentage (Sandhu et al., 2015). Three most effective grain yield QTLs, qGY1,1, qGY6,1 and qGY10,1, showed a consistent expression under DDSR conditions (Sandhu et al., 2013, 2015). The first QTL, qDTY12.1, reported for rice grain yield under drought at reproductive-stage had shown significant and consistent grain yield under drought under both upland and lowland ecosystems in multiple environments (Bernier et al., 2007; Mishra et al., 2013). Sandhu et al. (2019a) performed GWAS on a complex mapping population for DDSR traits and identified grain yield QTL (chromosome 11) in close proximity of earlier identified yield and yield-related QTLs reported by Mondaca et al., 2001, for grain per plant (gpl1,1), 1000 grain weight (gw11,1, gw11,2) and yield per plant (ylp11,1, l). The identified QTLs for grain yield are most suitable for use in MAB for DDSR because of their consistent effects across genetic backgrounds and environments.

Other traits contributing yield under DDSR

Modified panicle and root architecture

Panicle architecture and intense root system in rice show positive correlation with grain yield and yield-contributing traits (Arai–Sanoh et al., 2014; Okada et al., 2018). Molecular mechanism of several genes influencing panicle architecture traits in rice is well characterized, viz. GN1A, APO1, DEP1, WFP, OsLG, FAV1 and qOPW1 (Ashikari et al., 2005; Huang et al., 2009; Ikeda-
Kawakatsu et al., 2009; Ishii et al., 2013; Miura et al., 2010; Okada et al., 2018; Yoshida et al., 2013). Recently, a GWAS on complex mapping population revealed co-location of QTLs for root traits with na1, OsiPT3 and ELS, OsNAR2.1 genes for root development and nitrate uptake, respectively (Sandhu et al., 2019a). Also, many significant and stable QTLs influencing panicle architecture (Deshmukh et al., 2010; Guo and Hong, 2010; Okada et al., 2018; Sun et al., 2017) and root structure (Ara-Sano et al., 2014; Sandhu et al., 2013, 2015, 2019a; Uga et al., 2013) are reported and being used for developing DDSR-suitled varieties (Sandhu et al., 2019b).

Abiotic and biotic stress tolerances/resistances

Drought, heat and cold stress are the major challenges for productivity under DDSR. Several stable QTLs for grain yield under abiotic stress, putative genes in those QTL regions and interaction between yield QTLs under stress are reported. Rice blast, bacterial blight (BB), brown plant hopper (BPH), gall midge (GM) and brown spot (BS) are major biotic constraints in rice. More than 100 major genes and over 350 QTLs for blast resistance (Chen et al., 2020), more than 44 (dominant and recessive) genes for BB resistance (Kim and Reinke, 2019), more than 11 genes and several QTLs for GM resistance (Zhou et al., 2020), 31 genes and number of QTLs for BPH resistance (Chen et al., 2020), and 12 QTLs for BS resistance (Mizobuchi et al., 2016) are reported. Major QTLs for biotic and abiotic stress and their donors to be used in the DDSR breeding programme are mentioned in Table 1.

Seed dormancy

Seed dormancy (SD) is one of the important agronomic traits affecting grain yield and quality. Developing cultivars with deep dormancy during the development stage and weak dormancy at germination is a challenge (Cheng et al., 2014; Mizuno et al., 2018). Sd1 is one of the most important QTLs for seed dormancy in rice which has been cloned (Sugimoto et al., 2010). Lu et al. (2011) reported two grain dormancy QTLs, qSdn-1 and qSdn-5, whose dormancy is easily breakable by dry heat treatment (50°C), indicating its favourable utilization in breeding programmes.

Grain quality and nutrition

The grain quality is primarily determined by grain appearance, cooking and eating quality (CEQ) parameters, and aroma. Several QTLsgenes are reported for grain quality traits in rice (Li et al., 2014; Wang et al., 2015; Wu et al., 2017) and grain nutrition (protein and micronutrient content) (Descalsota-Empelo et al., 2019; Dixit et al., 2019; Kashiwagi and Munakata, 2018). Several studies reported the presence of QTLs for CEQ in the vicinity of waxy locus, suggesting Wx locus as a key factor to control CEQ traits (Wang et al., 2019). The development of molecular markers for high grain quality and content of essential nutrients is underway to foster the breeding for nutrient-rich quality rice (Descalsota-Empelo et al., 2019). However, mapping of CEQ traits under DDSR and TPR situations needs to be compared, before directly utilizing them into the breeding programmes.

Genomic breeding for developing DDSR varieties

Currently, predominant efforts are laid down to test elite TPR varieties for performance under DDSR conditions, and few were found to be fairly suitable (Table 3). Several major effect stable QTLs and donors for the traits related to improving yield and adaptability under DDSR are identified (Table 1) and being utilized to develop DDSR-adapted breeding lines employing genomic-breeding approaches to possible release for commercial cultivation in future. In genomic-breeding approaches, multi-genomes data, knowledge resources, genes and technologies generated by genomic research are used for precise breeding programmes (Wing et al., 2018). The methods of genomic breeding, viz. marker-assisted selection (MAS), marker-assisted backcross breeding (MABB) and marker-assisted recurrent selection (MARS), have been used successfully in crop improvement programmes. Novel approaches, such as haplotype-based breeding (HBB), forward breeding (FB), genomic selection (GS) and speed breeding (SB), should be integrated with existing genomic-breeding methodologies to accelerate the precision and efficiency of genetic gain in crop breeding (Varshney et al., 2020).

Genomic selection (GS) has a potential to improve genetic gain and breeding efficiency. In GS, genotyping is not limited to a selected set of markers that tag putative genes, but rather breeding value (genome estimated breeding values – GEBVs) is predicted based on genome-wide marker data to avoid ascertainment bias and information loss (Lorenz et al., 2011). Spindel et al. (2015) performed GWAS in conjunction with GS on 363 elite breeding lines from IRRI’s irrigated rice breeding programme and reported genomic prediction models performing better than predictions based on pedigree data alone for yield, flowering time and plant height traits. The RR-BLUP was found to be the most efficient statistical method for grain yield estimation where no large effect QTLs were detected by GWAS. For flowering time where single large effect QTL was detected, the non-GS multiple linear regression (MLR) method performed better than GS model. For plant height where four mid-sized QTLs were detected by GWAS, random forest produced the most consistently accurate GS models. These findings suggest that GS can make it possible to track, accumulate and select for small effect QTLs in addition to large effect QTLs. They further suggested that GS, informed by GWAS interpretations of genetic architecture and population structure, can be an effective tool to increase the efficiency of rice breeding as genotyping is becoming cost effective. Recently, a robust genotypic platform, 1K-Rice Custom Amplicon (1K-RICA), is reported as an alternative cost-effective genotypic platform for indica rice breeding programmes, which can enhance the efficiency of MAS and GS in indica rice germplasm pools (Arbelaez et al., 2019).

Most of the DDSR suitable traits to improve yield are extremely complex in nature, and thus, combining QTLsgenes in the genetic background of modern high-yielding varieties is recommended. The introgression of major effect QTLsgenes and its combinations may not always explain the desired improvement due to various interactions occurring for a complex quantitative trait. Genomic interactions, epistasis, pleiotropy and linkage among or between introgressed loci, with the genetic background and environment, play an important role in deciding the performance of genomic-breeding-derived lines. The QTL pyramiding approach has potential to improve understanding of interactions among QTLs and also helpful in developing new strategies to enhance the efficiency of genomic-breeding programmes. The performance of NILs possessing various QTL combinations (qDTY1.1, qDTY2.1, qDTY2.2, qDTY3.1, qDTY3.2, qDTY6.1, qDTY12.1) determining yield under drought in different genetic backgrounds (IR64, TDK1-Sub1, Savitri, Samba Mahsuri) was reported to be strongly affected by interactions with genetic background loci (Sandhu et al., 2018; Yadav et al., 2019).
Table 3  Popular varieties adaptable for dry direct-seeded rice system

| Country      | Adaptable/released rice variety | Reference |
|--------------|--------------------------------|-----------|
| Japan        | RS-15, RS-20                   | Tanno et al. (2007), Harada et al. (2007) |
| Cambodia     | Koshihikari, W42, CAR 14        | Kumar et al. (2017) |
| India        | ARB 6, MAS 26, CR Dhan 200, CR Dhan 202, CR Dhan 205 | Gandhi et al. (2012), Kumar et al. (2017) |
| Philippines  | Sahod Ulan 12, IR70358-84-1-1, Katihan 1 | Kumar et al. (2017) |
| Bangladesh   | BRRI Dhan-33, BRRI Dhan-39, BRRI Dhan-44, Zata | Kumar and Ladha (2011) |
| South Korea  | Juin1                          | Choi et al. (2007) |
| China        | Anhui, Zhejiang, Hubei, Han Dao 502, Han Dao 297, Jiangsu, Yunnan | Liu et al. (2014) |
| Indonesia    | Memberamo                      | Setyanto et al. (2000) |
| Nepal        | Sona Masuli, Hardinath, Radha-4, Radha-11, Chaito 2, Tarahara 1 | Kumar and Ladha (2011), Kumar et al. (2017) |

Genomic breeding for DDSR-related traits

An increase in rice productivity through genomic-breeding approach by introgression of multiple traits for abiotic/biotic stresses as well as traits improving adaptability under DDSR is a feasible breeding strategy to adapt well with climate change. In this context, a complex crossing programme started at IRRI in 2014 to combine DDSR-suited traits (anaerobic germination, early vigour, nodal roots, nematode tolerance, early uniform emergence, lodging resistance, and grain yield) with biotic stress tolerance (blast, BPH, BB, GM) in the background of DDSR-suitable breeding lines. Developed lines were evaluated in multiple seasons under DDSR for identifying promising lines. The performance of multiple stress-tolerant lines bred through MAS and conventional breeding approach were compared with DDSR checks to identify the suitable lines for further testing under targeted environments. Better performing lines for yield potentiality equal or more than Katihan 1 (high-yielding released variety for DDSR in Philippines) under DDSR condition were identified and forwarded for further testing (Table 4) (unpublished).

A set of breeding lines generated by complex crosses (possessing DDSR suitable traits) were evaluated for yield performance and adaptability under direct-seeded aerobic condition, and high-yielding stable line IR 97041-8-1-1-1 (qAG9.1, qGm4/Xa4/ Xa21/Pita/qNR5.1) was identified (Sandhu et al., 2019b). It showed higher yields of 20.1%, 2.9%, 9.4%, 30.1% and 18.8% over Vandana, BRRI dhan, Hardinath, Tarahara and Sahbhagi dhan in the Philippines, Bangladesh, Nepal and India, respectively.

At IRRI South Asia hub Hyderabad (India), complex crosses were made among donors possessing QTLs for DDSR suitable traits, viz. qEUE11.1, qEUE2.1, qEVE5.1, qRHD1.1, qNR5.1, qLDG3.1, qLDG4.1, qCS1.1, qGYD1.1, qGYD2.1, qGYD3.1, qGYD4.1, qAG9.1, qAG9.2, P9, Gm4, Gm8, Bph3 and Bph17. The marker-assisted backcross breeding strategy is being implemented to pyramid these QTLs in the background of popular variety MTU1010. Also, the lines derived from forward breeding approach are being evaluated for yield performance under DDSR (unpublished).

Varieties suitable for DDSR condition

To overcome water scarcity and considering the need of DDSR adoption, several attempts were made globally to test yield performance of TPR varieties under DDSR system. Although varieties released for aerobic conditions were found to perform well under DDSR situations (Kumar et al., 2017) (Table 3), to achieve higher yield potential these varieties should possess DDSR suitable traits.

In Brazil, rice varieties possessing characteristics of the modern plant type, suitable for the direct-seeded condition with a yield potential of up to 6.0 t/ha have been achieved through a breeding programme (Guimaraes, 2000). In China, two varieties HD 297 and HD 502 (suitable for aerobic condition) showed higher yield (2-5%) under DDSR situations (Liu et al., 2014). These varieties have higher yields with stronger drought tolerance, resistance to blast, better grain quality and an ideal plant type (reduced plant height, increased lodging resistance, erect upper leaves), which proves their suitability for adoption under DDSR situation (Liu et al., 2014, 2015).

In India, National Rice Research Institute (NRRI), Cuttack, has released six rice varieties for direct-seeded aerobic conditions; CR Dhan 200, CR Dhan 201, CR Dhan 202, CR Dhan 203, CR Dhan 205 and CR Dhan 206 through advancement and multilocation evaluation of breeding lines developed at IRRI with the objective to combine DDSR adaptability traits from upland cultivars with high yield potential of lowland cultivars. University of Agricultural Sciences, Bangalore (India), has released three rice varieties for direct-seeded aerobic conditions, viz. ARB 6, MAS 26 and MAS 946-1 for Karnataka state which were found to provide good yield under DDSR (Gandhi et al., 2012). The APO and CT-6510-24-1-2 showed better yield under direct-seeded aerobic condition.
than upland and irrigated varieties (Atlin et al., 2006). A lowland semi-dwarf hybrid variety Magat (IR64616H) possessing superior plant characteristics yielded 5.3 t/ha under direct-seeded aerobic condition (George et al., 2002). The variety Sahod Ulan 12, CAR 14 and Tarahara 1 were found to be most suitable under DDSR in the Philippines, Cambodia and Nepal, respectively (Kumar and Ladha, 2011; Kumar et al., 2017).

### Transcending from QTLs GENES TO SUPERIOR HAPLOTYPES FOR DEVELOPING DDSR VARIETIES

Considering the paramount importance and need of DDSR varieties, efforts have been made in the recent years to identify QTLs/genes for DDSR favourable traits to pave the way for DDSR breeding programmes. The high-throughput genotyping technologies are providing novel tools and techniques to plant breeding researchers for genomic breeding. Identifying significant marker-trait associations, QTLs, candidate genes and superior haplotype for targeted trait has become easier with the advent of whole-genome sequencing and high-density SNP arrays. The genome-wide association study (GWAS) identifies specific functional genetic variants and QTLs that are linked to the phenotypic differences in a trait of interest to facilitate the trait detection and selection of genotypes possessing that trait. GWAS is an important tool in genomic-breeding as it enables breeders to make selection based on MTAs (marker-trait associations) as a response to the combined effect of all favourable alleles. Superior haplotypes of target trait can be identified from the phenotypic performance of the group of individuals sharing a haplotype (specific haplotype group), and assembled through ‘haplotype assembly’ approach (Bevan et al., 2017). Further, this approach can be utilized in crop improvement programme through haplotype-based breeding (Abbai et al., 2019).

Till date, only few studies on GWAS for root morphology, nutrient uptake, yield and yield-related traits in rice under dry direct-seeded cultivation systems are reported. Sandhu et al. (2016) used two BC$_1$F$_2$ breeding populations from the crosses Kali Aus/MTU1010 and Aus 276/MTU1010, to understand the relationship between root architectural plasticity and yield stability across different water and crop establishment treatments and identified two significant genomic loci as hot spots. Three root architectural plasticity traits were correlated with the same SNP marker at one hot spot and root architectural plasticity and grain yield correlated with the same SNP marker at the second hot spot identified in both the populations. Thus, identifying progenies possessing multiple superior haplotypes associated with various co-located traits can serve as novel breeding material for developing DDSR varieties.

Recently, Sandhu et al. (2019a) performed GWAS on a complex mapping population for 39 traits (9 seedling-establishment traits, 14 root and nutrient-uptake traits, 5 plant morphological traits, 4 lodging resistance traits and 7 yield and yield-contributing traits) and reported a total of 10 significant trait-SNP associations and 25 QTLs associated with 25 traits under DDSR. Further co-location of the SNPs related to root traits, nutrient uptake and yield under DDSR was confirmed by the significant positive correlation of root traits with higher nutrient uptake and grain yield. Similarly, in other study conducted for same traits on MAGIC population, Subedi et al. (2019) identified a total of 37 MTAs for 20 traits and 9 putative QTLs related to different DDSR traits, among which 15 MTAs were located in the proximity of earlier identified candidate gene. Further, they identified seven promising progenies with better root morphology, nutrient-uptake and higher grain yield to be deployed in developing DDSR varieties through genomic breeding.

Most of the QTLs, especially those with large effects, have been being functionally characterized, providing several opportunities to create favourable alleles (de novo) of functionally characterized genes and thus to develop precise and systemic breeding strategies. Recent advances in genomics offer unique opportunities to underpin superior haplotypes of key genes either identified by QTL mapping or GWAS. For instance, haplotype diversity of grain shape-related genes (Lu et al., 2013), superior haplotype for deep-water rice (Kuroha et al., 2018) and the haplotype of HKT gene family that contributes to salt tolerance (Mishra et al., 2016) were determined. In our previous study, haplotype diversity of 120 key genes influencing

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### Table 4 Grain yield advantage of multiple stress-tolerant lines bred through MAS and conventional breeding approach over the suitable check under DDSR at IRRI (unpublished data)

| Designation | Grain yield (Kg/ha (Lowland)) | Grain yield (Kg/ha (DDSR)) | % yield increase over Katihan 1 | % yield increase over UPLRI 7 |
|-------------|-----------------------------|---------------------------|-------------------------------|---------------------------|
| IR 64       | 4875                        | 4447                      | –                             | –                         |
| Swarna      | 6030                        | 4777                      | –                             | –                         |
| MTU 1010    | 5268                        | 5447                      | –                             | –                         |
| UPLRI7      | 4200                        | 5600                      | –                             | –                         |
| Sahod ulan 6| 6243                        | 5800                      | –                             | –                         |
| Katihan 1   | 5369                        | 5828                      | –                             | –                         |
| MAS-1       | –                           | 5838                      | 0.17                          | 4.25                      |
| MAS-2       | –                           | 5943                      | 1.9                           | 6.13                      |
| MAS-3       | –                           | 6109                      | 4.5                           | 9.09                      |
| IR 115844-B-B-101-3-2 | 7213                  | 6216                      | 6.2                           | 11                        |
| IR 115845-B-B-170-1-1 | 7224                  | 6519                      | 10.5                          | 16.41                     |
| IR 115845-B-B-307-1-1 | 7272                  | 6926                      | 15.85                         | 23.5                      |

MAS-1 (qDTY$_2$), + qDTY$_3$, + xa5 + Xa21 + BPH3 + PIta2 + qAG$_3$, + qNR$_1$, + qRHD$_1$, + qEMM1), MAS-2 (qDTY$_1$, + qDTY$_2$, + qGYN$_1$, + qRHD$_2$, + Xa4 + Bph3 + PIta2 + qAG$_2$, + PIta9), and MAS-3 (qDTY$_3$, + qNR$_3$, + Xa4 + Xa5 + Xa21 + PIta2 + PIta9: lines developed through MAS approach; Katihan 1: high-yielding released variety for DDSR in Philippines.)
yield and quality traits was harnessed across the entire 3K Rice Genomes Panel (3K-RGP) and also superior haplotype combinations were identified for developing tailored rice by haplotype-based breeding (Abbai et al., 2019). Similarly, it is also possible to identify superior haplotypes of already known and novel genes associated with the most influencing DDSR-related traits using an integrated pipeline involving GWAS and haplo-phenotype (haplotype-phenotype) analysis. These haplotypes can eventually be utilized to develop early emerging, early maturing, abiotic/biotic stress-tolerant and high-yielding lodging resistant rice varieties suitable for DDSR condition employing haplotype-based breeding.

**Conclusion and future perspectives**

The DDSR cultivation technologies are environment-friendly and resource-saving as it supports yield under limited availability of water and labour, and also mitigates greenhouse gas emissions. There are several advantages of DDSR over TPR, and efforts are being made to address the constraints in its adoption. Currently, the varieties bred or developed for TPR situations have shown a yield decline of 10-30% under DDSR. Research efforts to tackle the constraints in adoption of DDSR technology have led to the identification of donors and QTLs for various DDSR-suited traits such as early uniform emergence, anaerobic germination, early vegetative vigour, higher nutrient uptake through higher root length density, lodging resistance and grain yield under the dry direct-seeded situation. Genomic-breeding approaches are being adopted to make use of available information on traits and genes/QTLs to breed DDSR suitable varieties.

Although several QTLs for DDSR-suited traits are identified, their interaction effects (QTL-QTL, background and environment) are not well studied, hindering their effective utilization in the breeding programmes. Further extensive research is needed to identify consistent QTLs/gene for important traits, viz. optimal nutrient uptake, and improved tolerance to soil nutrient deficiency, nematode tolerance, premium grain quality and nutrition under DDSR. Effective utilization of advanced tools and techniques of genomics can foster DDSR genomic-breeding programmes. Certainly, in the coming years intensive efforts are required towards the identification of key genes and their superior haplotypes regulating major DDSR traits to make rice more adaptable to cultivation under direct seeding.

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**Conflict of Interest**

The authors declare no conflict of interest.

**Author contribution**

AK and VKS conceived the idea. VKS, DBS and RA planned and outlined the review. DBS, PKJ, UMS, PGK and CV collected materials. DBS, AKS, SA, AJ and SD conducted comparative studies on nutritional traits, biotic stress, Fe deficiency tolerance and yield traits under DSR and TPR. SY and NS conducted the genomic-breeding studies for DDSR traits. DBS wrote the manuscript. RA and DBS prepared figures and tables. AK and VKS finalized the manuscript. All authors approved the final version.

**References**

Abbai, R., Singh, V.K., Nachimuthu, V.V., Sinha, P., Selvaraj, R., Vipparla, A.K., Singh, A.K. et al. (2019) Haplotype analysis of key genes governing grain yield and quality traits across 3K RG panel reveals scope for the development of tailor-made rice with enhanced genetic gains. Plant Biotechnol. J. 17, 1612–1622.

Angaji, S.A., Septiningsih, E.M., Mackill, D.J. and Ismail, A.M. (2010) QTLs associated with tolerance of flooding during germination in rice (Oryza sativa L.). Euphytica, 172, 159–168.

Arar-Sanoh, Y., Takai, T., Yoshinaga, S., Nakano, H., Kojima, M., Sakakibara, H., Kondo, M. et al. (2014) Deep rooting conferred by deeper rooting 1 enhances rice yield in paddy fields. Sci. Rep. 4, 5563.

Arelaæez, J.D., Dwiyanti, M.S., Tandayu, E., Lantada, K., Jarana, A., Ignacio, J.C., Platten, J.D. et al. (2019) 1k-RiCA (1K-Rice Custom Amplicon) a novel genotyping amplicon-based SNP assay for genetics and breeding applications in rice. Rice 12, 55.

Ashikari, M., Sakakibara, H., Lin, S., Yamamoto, T., Takashi, T., Nishimura, A., Angeles, E.R. et al. (2005) Cytokinins oxidase regulates rice grain production. Science 309, 741–745.

Atlin, G.N., Lafitte, H.R., Tao, D., Laza, M., Amante, M. and Courtois, B. (2006) Developing rice cultivars for high-fertility upland systems in the Asian tropics. Field Crops Res. 97, 43–52.

Baltazar, M.D., Ignacio, J.C.I., Thomson, M.J., Ismail, A.M., Mendioro, M.S. and Septiningsih, E.M. (2014) QTL mapping for tolerance of anaerobic germination from IR64 and the aus landrace Nanhi using SNP genotyping. Euphytica, 197, 251–260.

Bernier, J., Kumar, A., Ramaiah, V., Spaner, D. and Atlin, G. (2007) A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. Crop Sci. 47, 507–516.

Bevan, M.W., Uauy, C., Wulff, B.B., Zhou, J., Krasilova, K. and Clark, M.D. (2017) Genomic innovation for crop improvement. Nature 543, 346–354.

Bhasin, H., Bhatia, D., Raghuvanshi, S., Lore, J.S., Sahi, G.K., Kaur, B., Vikal, V. et al. (2012) New PCR-based sequence-tagged site marker for bacterial blight resistance gene Xa38 of rice. Mol. Breed. 30, 607–611.

Cabasan, M.T.N., Kumar, A. and De Waele, D. (2018) Evaluation of resistance and tolerance of rice genotypes from crosses of Oryza glaberrima and O. sativa to the rice root-knot nematode, Meloidogyne graminicola. Trop. Plant Pathol. 43, 230–241.

Chauhan, B.S., Jablan, K. and Mahajan, G., eds. (2017) Rice production worldwide, vol. 247. Berlin: Springer.

Chen, Q., Zeng, G., Hao, M., Jiang, H. and Xiao, Y. (2020) Improvement of rice blast and brown planthopper resistance of PTGMS line C8155 in two-line hybrid rice through marker-assisted selection. Mol. Breed. 40, 21.

Cheng, J., Wang, L., Du, W., Lai, Y., Huang, X., Wang, Z. and Zhang, H. (2014) Dynamic quantitative trait locus analysis of seed dormancy at three development stages in rice. Mol. Breed. 34, 501–510.

Chin, J.H., Gamuyao, R., Dalid, C., Bustamam, M., Prasetyono, J., Moeljopawiro, S., Wissuwa, M. et al. (2011) Developing rice with high yield under phosphorus deficiency: Pup? sequence to application. Plant Physiol. 156, 1202–1216.

Choi, I., Jeong, O., Jeong, E., Kim, H., Kang, K., Ryu, H.Y., Yang, S.J. et al. (2017) Developing direct seeding* Juan1*. Korean J. Breed. Sci. 39, 588–589.

Dai, X., Wang, Y., Yang, A. and Zhang, W.H. (2012) OsMYB2P-1, an R2R3 MYB transcription factor, is involved in the regulation of phosphate-starvation responses and root architecture in rice. Plant Physiol. 159, 169–183.

De Andrade, A., Tulmann-Neto, A., Tacencio, F.A., Marschalek, R., Pereira, A., de Oliveira Neto, A.M., Scheuermann, K.K. et al. (2018) Development of rice...
et al. (1992) Genetics of tolerance to iron.

Harada, H., Kobayashi, H. and Shindo, H. (2007) Reduction in greenhouse gas emissions by no-tilling rice cultivation in Hachirogata polder, northern Japan: Genomics, 37, 53–67.

Joshi, E., Kumar, D., Lal, B., Nepalia, V., Gautam, P. and Vyas, A.K. (2013) Management of direct seeded rice for enhanced resource-use efficiency. Plant Knowledge J., 2, 119.

Kashiwagi, T. and Munakata, J. (2018) Identification and characteristics of quantitative trait loci for grain protein content, TGP12, in rice (Oryza sativa L.). Euphytica, 214, 165.

Kuri, V. and Ladha, J.K. (2011) Direct seeding of rice: recent developments and future research needs. In Advances in Agronomy, vol. 111, ( Sparks, D.L., eds), pp. 297–413. San Diego, CA, USA: Academic Press.

Kuri, V., Nadag, N., Yadv, S., Pradhan, S.K., Anandan, A., Pandit, E., et al. (2017) Rice varietal development to meet future challenges. In The Future Rice Strategy for India, (Mohanty, S., Chengappa, P.G., Murlivunjaya, L., Ladha, J.K., Baraah, S., Kannan, E. & Manjunatha, A.V., eds), pp. 161–220. London: Academic Press.

Kuroha, T., Nagai, K., Gamuyao, R., Wang, D.R., Furuta, T., Nakamori, M., et al. (2006) Locus DEP1. Plant Soil, 280, 41–47.

Li, Y., Fan, C., Xing, Y., Yun, P., Luo, L., Yan, B., Peng, B., et al. (2014) Chalk encodes a vacuolar H+–translocating pyrophosphatase influencing grain chalkiness in rice. Nat. Genet., 46, 398.

Liu, H., Saddam, H., Zheng, M., Sun, L., Shah, F., Huang, J., Cui, K., et al. (2014) Progress and constraints of dry direct-seeded rice in China. J. Food Agric. Environ., 12, 465–472.

Liu, H., Hussain, S., Zheng, M., Peng, S., Huang, J., Cui, K. and Nie, L. (2015) Dry direct-seeded rice as an alternative to transplantated-flooded rice in Central China. Agron Sustain. Dev., 35, 285–294.

Original page: Page 319 of Plant Biotechnology Journal, Volume 18, Issue 2, March 2020, Pages 2173–2186.
Loan, L.C., Ngn, V.T.T. and Du, P.V. (2006) Preliminary evaluation on resistance genes against rice bacterial leaf blight in Can Tho Province-Vietnam. Omorinice, 14, 44–47.

Lorenz, A.J., Chao, S., Asoro, F.G., Heffner, E.L., Hayashi, T., Iwata, H., Smith, K.P. et al. (2011) Genomic selection in plant breeding: knowledge and prospects. In Advances in Agronomy. (Sparks, D.L. eds), vol. 110, pp. 77–123. San Diego, CA: Academic Press.

Lu, B., Xie, K., Yang, C., Wang, S., Liu, X., Zhang, L., Jiang, L. et al. (2011) Mapping two major effect grain dormancy QTL in rice. Mol. Breed. 28, 453–462.

Lu, L., Shao, D., Qiu, X., Sun, L., Yan, W., Zhou, X., Yang, L. et al. (2013) Natural variation and artificial selection in four genes determine grain shape in rice. New Phytol. 200, 1269–1280.

Macedo, A.F. (2012) Abiotic stress responses in plants: metabolism to productivity. In Abiotic stress responses in plants, (Ahmad, P. and Prasad, M.N.V., eds), pp. 41–61. New York: Springer.

Maeda, H., Murata, K., Sakuma, N., Takei, S., Yamazaki, A., Kanir, M.R., Kawata, M. et al. (2019) A rice gene that confers broad-spectrum resistance to β-triketone herbicides. Science, 365, 393–396.

Mahajan, G., Sarlach, R.S., Lapinder, S. and Gill, M.S. (2011) Seed priming effects on germination, growth and yield of dry direct-seeded rice. J. Crop Improv. 25, 405–417.

Mahajan, G., Singh, K., Singh, N., Kaur, R. and Chauhan, B.S. (2018) Screening of water-efficient rice genotypes for dry direct seeding in South Asia. Arch. Agron. Soi Sci. 64, 103–115.

Merugumala, G.R., Satyanarayana, P.V., Name, C., Ravikumar, B.N.V.S.R., Ramana Rao, P.V., Pavana, L. and Deepika, V. (2019) Molecular breeding of “Swarna”, a mega rice variety for lodging resistance. Mol. Breed. 39, 55.

Mishra, K.K., Vikram, P., Yadaw, R.B., Swamy, B.M., Dixit, S., Dixit, S., Cruz, M.T.S. et al. (2013) qDTY 12 f.: a locus with a consistent effect on grain yield under drought in rice. BMC Genet. 14, 12.

Mishra, S., Singh, B., Panda, K., Singh, B.P., Singh, N., Misra, P., Rai, V. et al. (2016) Association of SNP haplotypes of HKT family genes with salt tolerance in Indian wild rice germplasm. Rice. 9, 15.

Miura, K., Ikeda, M., Matsubara, A., Song, X.J., Itou, M., Isano, K., Matsuoka, M. et al. (2010) OsSFR14 promotes panicle branching and higher grain productivity in rice. Nat. Genet. 42, 545.

Mizobuchi, R., Fukuoka, S., Tsushima, S., Yano, M. and Sato, H. (2016) QTLs for resistance to major rice diseases exacerbated by global warming: brown spot, bacterial seedling root, and bacterial grain rot. Rice. 9, 23.

Mizuno, Y., Yamanoouchi, U., Hoshino, T., Nonoue, Y., Naigata, K., Fukuoka, S., Ando, T. et al. (2018) Genetic dissection of pre-harvest sprouting resistance in an upland rice cultivar. Breed. Sci. 68, 200–209.

Mochizuki, S., Jikumaru, Y., Nakamura, H., Koiwai, H., Sasaki, K., Kamiya, Y., Ichikawa, H. et al. (2014) Ubiquitin ligase ELS maintains the viability of root meristems by influencing cytokinin-mediated nitrogen effects in rice. J. Expt. Bot. 65, 2307–2318.

Moncada, P., Martinez, C.P., Borrello, J., Chatel, M., Gauch, H. Jr, Guimaraes, M. et al. (2001) Quantitative trait loci for yield and yield components in Oryza sativa L. Theor. Appl. Genet. 102, 41–52.

Okada, S., Sasaki, M. and Yamasaki, A. (2018) A novel rice QTL qPW11 associated with panicle weight affects panicle and plant architecture. Rice. 11, 1–9.

Okami, M., Kato, Y. and Yamagishi, J. (2011) Role of early vigor in adaptation of rice to water-saving agricultural culture: effects of nitrogen utilization and leaf growth. Field Crops Res. 124, 124–131.

Ookawa, T., Hoho, T., Yano, M., Murata, K., Ando, T., Miura, H., Anaso, K. et al. (2010) New approach for rice improvement using a pleiotropic QTL gene for lodging resistance and yield. Nat. Commun. 1, 132.

Ookawa, T., Inoue, K., Matsuo, M., Ebihara, T., Takarada, T., Yamamoto, T., Ueda, T. et al. (2014) Increased lodging resistance in long-culm, low-lignin gh2 rice for improved feed and bioenergy production. Sci. Rep. 4, 6567.

Piao, Z., Wang, W., Wei, Y., Zonta, F., Wan, C., Bai, J., Wu, S. et al. (2018) Characterization of an acetohydroxy acid synthase mutant conferring tolerance to imidazolinone herbicides in rice (Oryza sativa). Planta, 247, 693–703.

Qi, Y., Wang, S., Shen, C., Zhang, S., Chen, Y., Xu, Y., Liu, Y. et al. (2012) OsArf71, a transcription activator on auxin response gene, regulates root elongation and affects iron accumulation in rice (Oryza sativa). New Phytol. 193, 109–120.

Rao, A.N., Brainard, D.C., Kumar, V., Ladha, J.K. and Johnson, D.E. (2017) Preventive weed management in direct-seeded rice: Targeting the weed seedbank. In Advances in Agronomy. (Sparks, D.L., eds), vol. 144, pp. 44–142. Cambridge, MA: Academic Press.

Rehman, H.U., Azziz, T., Farooq, M., Wakeel, A. and Rengel, Z. (2012) Zinc nutrition in rice production systems: a review. Plant Soil. 361, 203–226.

Sanada, V.S.A.K., Himabindu, K., Naik, S.B., Sundaram, R.M., Vikrathamath, B.C. and Bentur, J.S. (2012) Mapping and marker-assisted breeding of a gene allelic to the major Asian rice gall midge resistance gene Gm8. Euphytica, 187, 393–400.

Sandhu, N., Jain, S., Kumar, A., Mehla, B.S. and Jain, R. (2013) Genetic variation, linkage mapping of QTL and correlation studies for yield, root, and agronomic traits for aerobic adaptation. BMC Genet. 14, 104.

Sandhu, N., Torres, R.D., Sta Cruz, M.T., Maturan, P.C., Jain, R., Kumar, A. and Henry, A. (2015) Traits and QTLs for development of dry direct-seeded rainfed rice varieties. J. Expt. Bot. 66, 225–244.

Sandhu, N., Raman, K.A., Torres, R.R., Audebert, A., Dardou, A., Kumar, A. and Henry, A. (2016) Rice root architectural plasticity traits and genetic regions for adaptability to variable cultivation and stress conditions. Plant Physiol. 171, 2562–2576.

Sandhu, N., Dixit, S., Swamy, B.M., Vikram, P., Venkateshwarlu, C., Catolos, M. and Kumar, A. (2018) Positive interactions of major-effect QTLs with genetic background that enhances rice yield under drought. Sci. Rep. 8, 1626.

Sato, H., Ando, I., Hirabayashi, H., Takeuchi, Y., Arase, S., Kihara, J., Kato, H. et al. (2008) QTL analysis of brown spot resistance in rice (Oryza sativa L.). Breed. Sci. 58, 93–96.

Sato, H., Satake, K., Ota, C., Yamakawa, T., Kihara, J. and Mizobuchi, R. (2015) Confirming a major QTL and finding additional loci responsible for field resistance to brown spot (Bipolaris oryzae) in rice. Breed. Sci. 65, 170–175.

Setniprothong, E.M., Ignacio, J.C.I., Sendon, P.M., Sanchez, D.L., Ismail, A.M. and Mackill, D.J. (2013) QTL mapping and confirmation for tolerance of anearobic conditions during germination derived from the rice landrace Ma-Zhan Red. Theor. Appl. Genet. 126, 1357–1366.

Setyanto, P., Makarim, A.K., Fagi, A.M., Wasmann, R. and Buendia, L.V. (2000) Crop management affecting methane emissions from irrigated and rainfed rice in Central Java (Indonesia). Nutr Cycling Agroecosyst. 58, 85–93.

Shikari, A.B., Khanna, A., Krishnan, S.G., Singh, U.D., Rathour, R., Tonapi, V., Sharma, T.R. et al. (2013) Molecular analysis and phenotypic validation of a novel herbicide (Imazethapyr) tolerant mutant in rice (Oryza sativa L.). Rice, 10, 10.
Singh, U.M., Yadav, S., Dixit, S., Ramaya, P.J., Devi, M.N., Raman, K.A. and Kumar, A. (2017) QTL hotspots for early vigor and related traits under dry direct-seeded system (Oryza sativa L.). Front. Plant Sci. 8, 286.

Spindel, J., Begum, H., Akdemir, D., Virk, P., Collard, B., Redona, E., Atlin, G. et al. (2015) Genomic selection and association mapping in rice (Oryza sativa): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding lines. PLoS Genet. 11, e1004982.

Subedi, S.R., Sandhu, N., Singh, V.K., Sinha, P., Kumar, S., Kumar, S., Singh, S.P. et al. (2019) Genome-wide association study reveals significant genomic regions for improving yield, adaptability of rice under dry direct seeded cultivation condition. BMC Genom. 20, 471.

Sudianto, E., Beng-Kah, S., Ting-Xiang, N., Saldain, N.E., Scott, R.C. and Sugimoto, K., Takeuchi, Y., Ebana, K., Miyao, A., Hirochika, H., Hara, N., Tanno, H., Aikawa, M., Yamazaki, N., Moriwaki, R. and Amano, T. (2007) qDTY 1.1, a major QTL for rice grain yield under reproductive-stage drought stress with a consistent effect in multiple elite genetic backgrounds. BMC Genet. 12, 89.

Wang, S., Li, S., Liu, Q., Wu, K., Zhang, J., Wang, S., Wang, Y. et al. (2015) The OsSPL16-GW7 regulatory module determines grain shape and simultaneously improves rice yield and grain quality. Nat. Genet. 47, 949.

Wang, H., Zhu, S., Dang, X., Liu, E., Hu, X., Eltahawy, M.S., Zaid, I.U. et al. (2019) Favorable alleles mining for gelatinization temperature, gel consistency and amylose content in Oryza sativa by association mapping. BMC Genet. 20, 34.

Wing, R.A., Purugganan, M.D. and Zhang, Q. (2018) The rice genome revolution: from an ancient grain to green super rice. Nat. Rev. Genet. 19, 505–517.

Wu, W., Liu, X., Wang, M., Meyer, R.S., Luo, X., Ndjonjdjop, N., Tan, L. et al. (2017) A single-nucleotide polymorphism causes smaller grain size and loss of seed shattering during African rice domestication. Nat. Plants, 3, 17064.

Xue, Y., Xia, H., Christie, P., Zhang, Z., Li, L. and Tang, C. (2016) Crop acquisition of phosphorus, iron and zinc from soil in cereal/legume intercropping systems: a critical review. Annal. Bot. 117, 363–377.

Yadav, S., Singh, U.M., Naik, S.M., Venkateshwarlu, C., Ramayya, P.J., Raman, K.A., Sandhu, N. et al. (2017) Molecular mapping of QTLs associated with lodging resistance in dry direct-seeded rice (Oryza sativa L.). Front. Plant Sci. 8, 1431.

Yadav, S., Sandhu, N., Majumder, R.R., Dixit, S., Kumar, S., Singh, S.P., Mandal, N.P. et al. (2019) Epistatic interactions of major effect drought QTLs with genetic background loci determine grain yield of rice under drought stress. Sci. Rep. 9, 1–13.

Yano, K., Oookawa, T., Aya, K., Ochiai, Y., Hiratsawa, T., Ebitani, T., Takarada, T. et al. (2015) Isolation of a novel lodging resistance QTL gene involved in strigolactone signaling and its pyramiding with a QTL gene involved in another mechanism. Mol. Plant, 8, 303–314.

Ye, C., Argayo, M.A., Redona, E.D., Sierra, S.N., Laza, M.A., Dilla, C.J., Mo, Y. et al. (2012) Mapping QTL for heat tolerance at flowering stage in rice using SNP markers. Plant Breed. 131, 33–41.

Ye, C., Tenorio, F.A., Argayo, M.A., Laza, M.A., Koh, H.J., Redona, E.D., Jagadish, K.A. et al. (2015) Identifying and confirming quantitative trait loci associated with heat tolerance at flowering stage in different rice populations. BMC Genet. 16, 41.

Yoshida, A., Sasa, M., Yasuno, N., Takagi, K., Daimon, Y., Chen, R., Yamazaki, R. et al. (2013) Tawawa1, a regulator of rice inflorescence architecture, functions through the suppression of meristem phase transition. Proc. Natl Acad. Sci. USA, 110, 767–772.

Zhang, Y., Tan, L., Zhu, Z., Yuan, L., Xie, D. and Sun, C. (2015) Torn1 confers tolerance to nitrogen deficiency in rice. Plant J. 81, 367–376.

Zhou, H., Wang, X., Mo, Y., Li, Y., Yan, L., Li, Z., Shu, W. et al. (2020) Genetic analysis and fine mapping of the gall midge resistance gene GmS in rice (Oryza sativa L.). Theor. Appl. Genet. 12, 1–13.