Identification of Markers for Root Traits Related to Drought Tolerance Using Traditional Rice Germplasm

Harendra Verma1 · R. N. Sarma1

Received: 6 March 2021 / Accepted: 10 August 2021 / Published online: 16 August 2021
© The Author(s), under exclusive licence to Springer Science+Business Media, LLC, part of Springer Nature 2021

Abstract

Drought is one of the important constraints affecting rice productivity worldwide. The vigorous shoot and deep root system help to improve drought resistance. In present era, genome-wide association study (GWAS) is the preferred method for mapping of QTLs for complex traits such as root and drought tolerance traits. In the present study, 114 rice genotypes were evaluated for various root and shoot traits under water stress conditions. All genotypes showed a significant amount of variation for various root and shoot traits. Correlation analysis revealed that high dry shoot weight and fresh shoot weight is associated with root length, root volume, fresh root weight and dry root weight. A total of 11 significant marker-trait associations were detected for various root, shoot and drought tolerance traits with the coefficient of determination ($R^2$) ranging from 18.99 to 53.41%. Marker RM252 and RM212 showed association with three root traits which suggests their scope for improvement of root system. In the present study, a novel QTL was detected for root length associated with RM127, explaining 19.30% of variation. The marker alleles with increasing phenotypic effects for root and drought-tolerant traits can be exploited for improvement of root and drought tolerance traits using marker-assisted selection.

Keywords Root traits · Drought tolerance · SSR marker · Rice and GWAS

Introduction

Drought is the major abiotic stress that deleteriously affects rice productivity in the rainfed ecosystem [1]. In Asia, around 42 million hectares of rice cultivation out of total 163 million hectare rice cultivation is negatively affected by drought and this situation is worsening under the regime of climate change which further may likely to increase moisture stress intensity, duration and frequency [2–4]. Drought stress significantly reduces rice yield from 25 to 50% [5, 6] and causes an economic loss of $37 billion [7]. Reduced rice yield poses threats to global food security and sustainable development [5, 7, 8, 9]. The ceiling in rice productivity has been observed, which indicates the inadequacy to meet the future rice demand of the ever-growing population. Therefore there is a need to improve the productivity of rice cultivated in drought-prone areas. This has necessitated the development of drought-tolerant varieties to combat the moisture stress problem. Breeding for the development of drought-tolerant variety is the greatest challenge and priority.

Rice productivity in rainfed areas of the world can be enhanced in sustainable ways with genetic improvement of drought tolerance and root traits [10, 11]. The root system is the foremost important plant organ which sense and responds to soil moisture stress and helps in the absorption of various nutrients and water from the soil for normal plants growth and development [12–15]. Various root characteristics help in maintaining the plant productivity under drought are long specific root length, small fine root diameter and considerable root length density in deeper soil horizons, where an ample amount of moisture is available [14, 16, 17]. Among rice genotypes, huge genetic variation is exists for root depth and various root traits [16]. However, little progress has been made in characterizing the genetic determinants of root traits in relation to drought tolerance. Genetic improvement of root traits through conventional breeding is challenging and limited because roots are underground parts and screening is highly labor-intensive and difficult to use in large mapping.
populations. A study related to the detection of QTLs associated with root traits under water stress and drought tolerance using rice genotypes from North East India has not been carried out, which provides the opportunities for GWAS to supplement the drought tolerance improvement breeding. The use of molecular markers is the best tool to support phenotypic selection. Identification of drought-related QTLs (qDTY1.1) for grain yield [18], Dro1 QTL [19] for root angle and their use in marker-assisted breeding is a hope to develop high yielding drought-tolerant rice varieties. QTLs associate with root traits and drought tolerance have been identified in rice and successfully introgressed using marker-assisted technology into rice elite breeding lines for improvement of root traits and development of drought-tolerant variety [20–23]. Marker-assisted breeding (MAB) can improve the efficiency of plant breeding through the precise transfer of genomic regions of interest and fast recovery of the recurrent parent genome in lesser time as compared to conventional breeding methods [24]. Therefore, the identification of DNA markers associated with root traits and drought tolerance traits and their use in marker-assisted selection is the best tool to relieve this bottleneck.

The use of identified markers linked to a particular QTL using biparental mapping population is limited to a population of a specific cross and requires validation in a new population. The estimated effect of QTLs are also inconsistent in the different genetic background [25, 26] and poor linkage between QTLs and markers limits their use in MAB [27–29]. Therefore to circumvent the limitation of QTL mapping, GWAS are considered as a potentially powerful approach for mapping causal genes with modest effects [30]. The GWAS utilizes the broader genetic variations with wider background for marker traits association and identified markers have a strong linkage with traits. Identification of markers associated with root traits and drought tolerance in diverse rice landraces set will help in stable estimation of the genetic basis and their application may increase the improvement of root and drought tolerance.

North-Eastern India is one of the hot spots of rice genetic resources in the world [31]. The upland rice cultivated from March to July in this region is known agronomically as “aus/ahu” rice. Recently, based on genome sequence information, aus subpopulation is identified as distinct subpopulation of O. sativa species [32, 33] and suggested that aus cultivars evolved from a distinct population of the annual Oryza nivara found in NE India, Bangladesh and Northern Myanmar [34, 35]. The upland landraces of rice present in northeast India are drought-tolerant, photoperiod insensitive has better root system and resistant to diseases [16, 36, 37]. For example, Aus 196, an improved drought-tolerant cultivar belongs to aus subspecies and originated from Eastern India [38, 39]. Drought-tolerant genotypes ‘Banglami’ and ‘Inglongkiri’ were identified from Assam [16] and http://dbtaau.ac.in/allele.html]. Therefore, it is expected that the germplasm from North-Eastern India might provide new genes/alleles for the improvement of drought tolerance via a better root system.

Thus in the present study, an attempt has been made to detect the significant major QTLs associated with root traits and drought tolerance through GWAS using Northeast India traditional rice germplasm. So that, identified candidate genes can be used for the improvement of drought tolerance in rice using MAB technology.

**Materials and Methods**

**Plant Materials and Phenotypic Evaluation**

The present study material consists of 114 rice genotypes of Northeast India involving Ranjit, IR-64 and Manohar Sali HYVs which flowered with in a range of 10–15 days to get the homogeneity in the other data. Pure and healthy seeds of 114 rice landraces were obtained from Regional Agricultural Research Station (RARS) Titabar farm of Assam Agricultural University, Jorhat. These rice genotypes were directly sown in moist soil in three replications and evaluated for various root and drought tolerance traits at reproductive stage in PVC pipes using completely randomized block design (CRBD design under a rain shelter at Instrumental cum Research (ICR) farm of Assam Agricultural University, Jorhat. All genotypes were phenotyped for root length (RL), root volume (RV), fresh root weight (FRW), dry root weight (DRW), root angle (RA), bottom root number (BRN), peripheral root number (PRN), shoot length (SL), dry shoot weight (DSW), fresh shoot weight (FSW), root to shoot ratio (RSR), ratio of deep rooting (RDR), leaf rolling score (RLS) and drought recovery (DR) (Table 1). Drought was induced by withdrawing the life-saving irrigation 13 days after sowing (DAS). The observation for drought tolerance was recorded during noon hours at 32 and 34 days after withdrawal of life-saving irrigation (DAWW) when the soil moisture content was around 7–8% (W/V) and susceptible check (IR64 and Ranjit) showed complete drought stress symptoms using "Standard Evaluation System for Rice (SES)" of IRRI [40]. The soil moisture status was determined using the gravimetric method of Reynolds [41]. The root length, shoot length, fresh root weight and shoot weight data of 46-day-old plants of stress experiment was recorded using PVC pipes following the standard method. Root dry weight and shoot dry weight were recorded after consistent drying of plant samples for 7 days at 80 °C. The basket method of Uga [19] was used to measure root angle, bottom root number and peripheral root number. Baskets were filled with sieved soil free of the root of weeds and no fertilizer was applied.
SSR Genotyping

Initially, a total of 170 SSR markers involving 30 gene-specific markers related to root and aquaporins, covering all 12 chromosomes, located at 5 cm interval were assessed for genotyping of 114 rice genotypes. Finally, we retained 65 SSR markers including four gene-specific markers based on prominent distinguishable banding patterns, polymorphism and no missing data to increase the reliability of results. The genetic sequence of genes related to root traits and drought tolerance factors were downloaded from http://rapdb.dna.affrc.go.jp/ and http://rice.plantbiology.msu.edu/. Gene-specific primers were designed using Primer 3 software. SSR marker sequences, annealing temperature and chromosomal locations were obtained from the GRAMENE database.

Genomic DNA was isolated from fresh leaves of each genotype included in the present study following the protocol of Plaskhe [42] with slight modification. The quality of DNA was determined by comparing the genomic DNA with uncut-lambda DNA marker in 1% agarose gel and; quantity was determined using nano-drop reading at 260 nm. The final concentration of DNA was adjusted to 30 ng/μl for PCR reaction. The amplification conditions were based on the procedure of Panaud [43]. The PCR reaction volume was 10 μl. The PCR reaction mixture of 10 μl consists of 0.4mM dNTPs, 4 mM of MgCl2, 150 mM of Tris–HCl, 10 pmol of forward and reverse primer and 0.05 U Taq polymerase with 30 ng of DNA. The reagents were mixed thoroughly and then placed in a Thermal Cycler (PCR Gene AMP® 2400, Applied Biosystems, USA) for cyclic amplification using the amplification program Step 1 (Initial denaturation) 94 °C for 5 min. Step 2 (Denaturation) 94 °C for 1 min. Step 3 (Annealing) 32 °C for 1 min. Step 4 (Extension) 72 °C for 1 min. Step 5 (Final extension) 72 °C for 5 min. Step 6 (Storage) 4 °C for infinity. Steps 2, 3 and 4 were repeated 35 times.

Gel Electrophoresis, Photography and Allele Scoring

Amplified alleles were separated based on their size using 3% agarose gel and 1×TBE buffer in the horizontal electrophoresis tank, after this the gel image was digitally documented in Gel Documentation System (UVP, UK). The size of distinct amplified bands was measured in base pair by comparing with the band size of 100 bp ladder (GeneI Company) with IR-36 as molecular weight reference.

Data Analysis

The mean of root and drought tolerance data recorded from genotypes were subjected to analysis of variance (ANOVA), genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), broad sense heritability and genetic advance as 5% of the mean (GA) using SPAR 2.0 software [44]. R software packages corplot [45] and RColorBrewer [46] were used for calculation and visualization of the Pearson’s correlation. Association analysis between marker loci and phenotypic traits was performed in all trials using

| Parameter traits | Range | Mean ± SEM | CD 5% | GCV    | PCV    | $h^2$ (Broad sense) | GA as % of mean (5%) |
|------------------|------|-----------|------|--------|--------|---------------------|----------------------|
| DS 32 DAW        | 0.04 | 0.95      | 0.83±0.02 | 0.05     | 27.83  | 28.13               | 0.98                 | 56.70                |
| DS 34 DAW        | 0.04 | 0.95      | 0.90±0.01 | 0.03     | 20.58  | 20.71               | 0.99                 | 42.14                |
| Recovery         | 0.04 | 0.95      | 0.44±0.02 | 0.07     | 90.32  | 90.84               | 0.99                 | 185.00               |
| RL (cm)          | 7.00 | 25.50     | 12.60±0.54 | 1.49     | 25.20  | 26.26               | 0.92                 | 49.84                |
| SL (cm)          | 30.00 | 94.33    | 56.03±2.01 | 5.6      | 23.54  | 24.35               | 0.94                 | 46.89                |
| FRW (gm)         | 0.07 | 8.57      | 0.70±0.17 | 0.47     | 122.05 | 128.80              | 0.90                 | 238.24               |
| DRW (gm)         | 0.02 | 2.49      | 0.22±0.09 | 0.25     | 111.22 | 131.22              | 0.72                 | 194.19               |
| FSW (gm)         | 0.15 | 10.03     | 1.87±0.36 | 0.99     | 86.83  | 92.92               | 0.87                 | 167.12               |
| DSW (gm)         | 0.03 | 2.82      | 0.45±0.12 | 0.34     | 82.31  | 94.56               | 0.76                 | 147.61               |
| RV (ml)          | 0.07 | 8.65      | 1.20±0.35 | 0.99     | 77.77  | 93.01               | 0.70                 | 133.94               |
| RA (°)           | 16.00 | 92.00    | 49.66±4.27 | 11.9  | 29.05  | 32.64               | 0.79                 | 53.24                |
| PRN              | 6.67 | 55.00     | 21.96±2.64 | 7.36     | 36.18  | 41.76               | 0.75                 | 64.57                |
| BRN              | 0.00 | 40.00     | 11.10±1.68 | 4.68     | 41.52  | 49.09               | 0.72                 | 72.33                |
| RSR              | 0.14 | 0.49      | 0.23±0.01 | 0.03     | 28.17  | 29.38               | 0.92                 | 55.65                |
| RDR              | 0.00 | 0.81      | 0.34±0.04 | 0.11     | 30.00  | 36.35               | 0.68                 | 51.00                |

Mini, minimum; Max, maximum; SEm standard error of mean; CD critical difference; $h^2$ heritability; GA genetic advance, DS 32 DAW drought score 32 days after withdrawal of water, DS 34 DAW drought score 34 days after withdrawal of water, RL root length, SL shoot length, FRW fresh root weight, DRW dry root weight, FSW fresh shoot weight, DSW dry shoot weight, RV root volume, RA root angle, PRN periphery root number, BRN bottom root number, RSR root to shoot ratio, RDR ratio of deep rooting
Algorithm [48]. It has been reported that the Q + K model reduces the false positive associations [49]. Hence, the results of MLM which uses the Q + K model are reported in the study. The marker P value (0.001) was used to determine the significance of each marker-trait association.

Results

Root, Shoot and Drought Tolerance Traits

The mean values of the root, shoot and drought tolerance traits and genetic parameters of 114 rice genotypes are given in Table 1. In water stress condition, among the genotypes, the highest root length was recorded in Inglongkiri (25.50 cm) while the lowest root length (7.00 cm) was recorded in Ranga Sali-2 with an average root length of 12.60 cm. The fresh shoot weight ranged from 0.09 g in Miren Killak to 8.57 g in Inglongkiri, with a mean fresh root weight of 0.70 g. Similarly, dry root weight varied from 0.02 g for AS-69-70 to 2.49 g for Inglongkiri with an overall mean of 0.22 g. Root volume ranged from 0.08 ml for Ahu Joha to 8.65 ml for Inglongkiri. The highest root angle was recorded in Kosamoni (64°) while the lowest root angle (16°) was recorded in Norin18/Patnai23 and Ranga Sali-2 with an average root angle of 47°. The wide range of variation for root length, root weight, root volume, root angle revealed the scope for selection for the development of genotypes with the better root system. The minimum periphery root number 7 was recorded in Norin18/Patnai23 while the maximum periphery root number 55 was recorded in Nepali Sali (55), with a mean of 22. The bottom root number ranged from 0 for Boga Gajep to 40 for As 193/1, with a mean of 11. Among genotypes, the highest root: shoot ratio was recorded in Dusri Ahu (0.49) and the lowest root: shoot ratio recorded in searcher (0.14) and Kacher Sali (0.14), with a mean of 0.23. Highest ratio of deep rooting was recorded in As 193/1 (0.81) while the lowest ratio of deep rooting was recorded in Boga Gajep (0), with a mean of 0.34. Maximum bottom root number and highest ratio of deep rooting were observed in As 193/1, but it showed drought susceptible response based on leaf rolling score.

In stress condition, the maximum shoot length was recorded in Horin Kajuli (94.33 cm) while lowest shoot length was recorded in Lachit and Raja Ahu (30 cm) with a mean shoot length of 56.03 cm. Genotypes having long shoot length showed long root system, for example, genotypes ARC10372, Banglami, Inglongkiri, December Sali-1, Goruntia Ahu, Horin Kajuli, Hafa Ahu and Ikora Guni showed long shoot length and long root system. Selection of these genotypes having tall and thick stem might help in increasing root length and drought tolerance. Fresh shoot weight ranged from 0.15 g for Miren Killak to Horin Kajuli 10.03 g. Fresh shoot weight had an overall mean of 1.86 g and Horin Kajuli significantly differed from all other genotypes for fresh shoot weight. Genotypes showing high long shoot weight showed high long root weight. Among the genotypes, dry shoot weight ranged from 0.03 g for Miren Killak to 2.82 g for Inglongkiri, with a mean dry weight of 0.45 g. Inglongkiri was significantly superior for dry shoot weight among all genotypes. Among 114 genotypes under study, nine genotypes showed a leaf rolling score of 0 indicating drought-tolerant and 18 genotypes showed a leaf rolling score of 5 and 3 suggesting moderately drought-tolerant. Thirteen genotypes showed the leaf rolling score of 7 which indicated moderate susceptibility of genotypes towards drought and 74 genotypes showed leaf rolling scoring of 9 which indicated susceptibility towards drought.

In the present study material Inglongkiri, Banglami, ARC10372, Bizor and Horin Kajuli are the promising genotypes that showed better root system and drought tolerance response to be used in the breeding program for improvement of drought tolerance. Improvement of the root system and drought tolerance would be the key to develop elite rice varieties suitable for the water-saving farming system.

Genetic Variability for Root, Shoot and Drought Tolerance Traits

The study of genetic variation and identification of promising genotypes with the desired root system might help breeding programs in the development of drought-tolerant rice. The estimate of the genotypic and phenotypic coefficient of variation, heritability in broad sense and expected genetic advance as a percentage mean expected at 5% for the characters are presented in Table 1. In all these characters’ under-study, GCV had a close correspondence with PCV along with high heritability estimates indicating less influence of environmental factors and predominance of an additive gene effect. The analysis revealed the existence of a very high genotypic coefficient of variation for all parameters.

Broad sense heritability was found higher for all characters. Maximum broad sense heritability recorded for recovery (98.90%) followed by drought scores at different days after withdrawal of water (98.80%) and shoot length (93.50%) respectively. Genetic advance as a percentage of mean was observed higher (> than 42%) for all the characters. The maximum genetic advance was observed for fresh root weight (238.24%) followed by dry root weight (194.19%) and recovery (185.00%), respectively. All these characters exhibited high genetic gain along with high heritability indicating a preponderance of additive gene action.
Recovery, fresh root weight, dry root weight, fresh shoot weight, dry shoot weight and root volume trait are the best to use in breeding considering GCV, heritability and genetic advance. The present findings for root system variation suggested the possibility for the development of variety with a better root system having drought tolerance using the existing variability.

Interrelationship Studies

The interrelationship analysis is presented in Fig. 1, and this analysis revealed that root length has a positive correlation with fresh root weight, dry root weight, fresh shoot weight, dry shoot weight and root volume. Selection for high dry shoot weight and fresh shoot weight help in the improvement of root length, root volume, fresh root weight and dry root weight, which leads to improvement in drought tolerance.

Root volume had a positive correlation with fresh root weight, dry root weight, dry shoot weight, fresh shoot weight and shoot length. Fresh root weight was positively correlated with dry root weight, dry shoot weight, fresh shoot weight and root length.

The ratio of deep rooting (RDR) showed a positive correlation with the number of bottom root number at the genotypic and phenotypic level, which is obvious because RDR is the proportion of the total number of roots penetrating the lower part of the mesh to the total number of roots penetrating the whole mesh. Therefore, as there is an increase in the number of bottom root numbers there will be an increase in RDR. Root: shoot ratio had a negative correlation with shoot length both at the genotypic and phenotypic level which is also obvious, as there is an increase in shoot length there will be a decrease in root/shoot ratio.

Marker-Trait Association Analysis

Population structure may lead to a spurious association between marker and traits. Therefore, to avoid spurious association genetic structure of the given population was identified using the software STRUCTURE version 2.3.4 [16]. The Q matrix generated in structure analysis was used for the

---

**Fig. 1** Pearson correlation coefficient between root, shoot and drought tolerance traits in rice. 
PRN periphery root numbers, RA root angle, RSR root shoot ratio, SL shoot length, FSW fresh shoot weight, DSW dry shoot weight, RL root length, DRW dry root weight, FRW fresh root weight, RV root volume, BRN bottom root numbers, RDR ratio of deep rooting, Rec recovery, DS_32 drought score 32 days after withdrawal of water, DS_34 drought score 34 days after withdrawal of water.
model-based general linear model (GLM) and mixed linear model (MLM) approach for association mapping. Marker trait association analysis using MLM model (mixed linear model) based on Q matrix generated in STRUCTURE and kinship matrix of TASSEL revealed a total of 11 associations at \( P < 0.0001 \) for eight roots, shoot and drought sensitivity traits with \( R^2 \) ranging from 18.99 to 58.11% under water stress situation without type 1 error (Table 2). In this study, both GLM and MLM tests showed different outcomes since GLM considers only population structure, whereas MLM uses both population structure and kinship for analyses.

One association was detected for recovery of 1st leaf one day after irrigation on chromosome 9 by RM24390 explaining 18.99% of the variation. The marker RM212 located on chromosome 1 showed association with dry root weight, fresh root weight and root volume explaining 33.96%, 31.79% and 30.83% of the variation, respectively. The marker RM252 on chromosome 4 was associated with dry root weight, fresh root weight, root volume, dry shoot weight and fresh shoot weight explaining 58.11%, 53.41%, 40.42%, 37.90% and 19.27% of the variance, respectively. Single marker RM418 on chromosome 7 was associated with root to shoot ratio with a variation of 23.27%. The marker RM127 on chromosome 4 was associated with root length explaining 19.30% of the variation.

### Allelic Effect of Linked Markers

The allelic effects, in terms of band size in bp, of different linked markers are depicted in the boxplot (Fig. 2). The RM24390 markers is associated with leaf recovery 55 DAS and two alleles were detected. The allele of 80 bp of RM24390 is associated with an increasing phenotypic effect by 10.7% on leaf recovery, whereas, the allele of 90 bp is associated with a decrease of leaf recovery by 25.24%.

The marker RM252 is associated with fresh shoot weight, dry shoot weight, root volume, dry root weight and fresh root weight. Three alleles were detected for RM252 marker. The allele of 170 bp of RM252 is associated with an increasing phenotypic effect of fresh shoot weight by 0.76 g, dry shoot weight by 0.19 g, root volume by 0.16 ml and fresh root weight by 0.16 g, whereas the allele of 155 bp associated with the decrease of fresh shoot weight by 0.40 g, dry shoot weight by 0.9 g, root volume by 0.2 ml and fresh root weight by 0.14 g. The marker RM212 is associated with root volume, fresh root weight and dry root weight and two alleles were detected. The allele of 145 bp of RM212 associated with the decrease of root volume by 0.07 ml dry weight by 0.1 g and dry root weight by 0.002 g. The marker RM418 is associated with root shoot ratio and two alleles were detected. The allele of 300 bp of RM418 is associated with decreasing phenotypic effect of root shoot ratio by 0.0004. The marker RM127 was associated with root length and two alleles were detected. The allele of 230 bp of RM12 is associated with increasing phenotypic effect of root length by 0.11 cm, whereas the allele of 270 bp is associated with a decrease of root length by 0.16 cm.

### Discussion

Identification and mapping of molecular markers significantly associated with traits of interest can help in the genetic improvement of cultivars through the deployment of marker-assisted breeding (MAB). MAB has enormous potential to transfer desirable traits from donor parent to recipient parent in less time through deployment of molecular markers associated with a trait of interest [39]. The recent advances in molecular breeding tools and techniques have been very useful in understanding the genetic basis of complex traits to identify major genes/QTLs for use in rice breeding [29].
Fig. 2 The allelic effects, in terms of band size in bp, of different linked markers.
Fig. 2 (continued)
under early stage water stress using the GWAS approach. The present study aimed to assess the drought-tolerant variety is most important under the regime for improvement of drought tolerance. The development of the genetic basis of drought tolerance in relation to root traits for the identification of genes/QTLs for root traits related to drought tolerance, which is a crucial step in understanding the genetic basis of drought, is explained by population structure analysis [54, 55]. The GWAS has been done using diverse genotypes. In GWAS the entire genome is to be assessed for trait-associated variants, rather than analyzing specific candidate genes [56]. The GWAS has been done for the identification of genes/QTLs for root traits related to drought tolerance, which is a crucial step in understanding the genetic basis of drought tolerance in relation to root traits for improvement of drought tolerance. The development of drought-tolerant variety is most important under the regime of climate change. The present study aimed to assess the genetic variation and identify markers for root shoot traits under early stage water stress using the GWAS approach.

**Marker Trait Association**

A total of 5 SSR markers were significantly associated with root, leaf recovery and shoot traits under water stress. One association was detected for the marker RM24390 on chromosome 9 associated with recovery of 2nd leaf one day after irrigation on chromosome 9 by RM24390 and explaining 19.05% of the variation. A promising QTL, qDTY9.1B was detected for grain yield under water stress associated with SSR marker interval between RM24350 (15.4 Mb) to RM24390 (15.9 Mb) [57] and this QTL did not show a positive effect on grain yield under the irrigated situation. The present study also confirmed the presence of QTLs near RM24390 for drought tolerance and which needs further analysis, though no published report available on the presence of QTL for drought sensitivity traits on this chromosome.

The marker RM212 located on chromosome 1 showed association with dry root weight, fresh root weight and root volume explaining 33.96%, 31.79% and 30.83% of variance, respectively. The marker RM212 was associated with root volume [58], root dry weight [59] in Zh97/Ming63 RI lines thereby confirming the association of RM212 with root volume and dry root weight QTLs. Similarly, Kamoshita [60] reported QTLs for root depth, penetrated root thickness, deep root to shoot ratio, deep root dry weight, deep root per tiller, and deep root mass to be associated with RM212 on chromosome 1 in CT9993/IR62266 DH lines, which also confirmed the association of RM212 with the QTLs for dry root weight. RM212 was reported to be linked with plant height, panicle length, shoot biomass, straw yield and harvest index under water stress [61]. Swamy [62] reported RM543–RM212 a small genetic distance of 0.27 kb associated with yield and drought tolerance in rice. Similarly, Kanagraj [63] reported that RM212 was associated with drought resistance traits. Gomez [64] reported RM212 to be associated with plant height and biomass under water stress. Zhao [65] found RM212 to be linked with stomatal conductance and transpiration rate under stress. Sabar [66] reported association of RM212-RM265 with plant height, the findings of Babu [67] suggested that RM212 was associated with RWC under drought stress. Salunke [68] reported that region RM212–RM302–RM8085–RM3825 on chromosome 1, harbors large effect QTLs for drought resistance traits across several genetic backgrounds in rice. SSR Marker RM212 has been used in MAS for introgression of qDTY2.1 and qDTY1.1 QTLs for drought tolerance improvement in rice [69]. The present study corroborated those results confirming the presence of QTLs for fresh root weight, dry root weight, root volume and dry shoot weight linked to RM212. However, the presence of QTLs for many traits identified with RM212, the possibility of pleiotropic effect or a closely linked gene complex, needs further analysis with a high density marker around this region.

Marker RM252 on chromosome 4 was associated with dry root weight, fresh root weight, root volume, dry shoot weight and fresh shoot weight explaining 58.11%, 53.41%, 30.83%, 37.90% and 19.27% of variance, respectively. Zheng [70] reported RM252 to be associated with root thickness and root penetration ability. Singh [71] reported validation of RM252 associated with root thickness and penetrating ability under drought situation in rice recombinant inbred lines (RILs). The present investigation also confirmed the associations of RM252 with root traits under water stress situation as similar QTLs were identified previously. The present study also detected the association of RM252 with...
shoot traits, it might be due to the pleiotropic effects of this marker on root and shoot traits or co-localization of root and shoot traits. The correlation coefficient analysis also revealed the association of root and shoot traits. Therefore, further confirmation is required with a high density marker around this region to ensure the pleiotropic effect or co-localization of markers for root and shoot traits on chromosome 4. The pleiotropic or co-localization of markers for root and shoot traits provide the opportunity to explore the collaborative development of root and shoot traits in rice [72].

In the present study RM127 located on chromosome 4 was associated with root length explaining 19.30% of variation. This marker was identified to be linked to spikelet fertility in rice [73]. Zhao [72] also reported root length QTL associated with RM1112 which is close to RM127 in indica rice species. Since, there is a dearth of information of any QTL for root length on chromosome 4, the QTL identified in the present study may be considered a novel for root length. Further analysis is required to validate the present findings.

One association was detected for root shoot: ratio on chromosome 7 by RM418 explaining 23.27% of variation. Zhao [72] reported the association of RM418 with overwintering germination ability. An [74] and Zheng [75] reported association with salt tolerance in rice. Association of RM418 was reported with grain quality traits such as paste viscosity [76] and protein content [77] in rice. Guo [78] reported association of RM418 with rice blast tolerance. GWAS study on yield traits by Eizenga [79] suggested association of RM418 with days to heading in rice. However, no published report was available to corroborate the presence of a QTL for root:shoot ratio linked to RM418, this QTL might be considered as novel QTL for root:shoot ratio. But more experiments are needed to confirm the validity of the QTL for root: shoot ratio as detected in the study.

The marker alleles which showed increasing phenotypic effects for root and drought-tolerant traits can be exploited through marker-assisted selection for improving root and drought tolerance of elite varieties. Though this study is based on limited numbers of SSR markers, this study highlighted the potentiality of the population to use as effective association mapping panel in identifying novel alleles/genes for improving traits related to root, shoot and drought tolerance.

**Phenotypic Variation and Potential for Genetic Improvement**

In the present study, significant variation for various root, shoot, drought sensitivity scores and recovery scores among rice genotypes indicated the scope of improvement in these traits using diverse germplasm. Similarly, variation for root traits such as root length, root biomass, root volume, roots to shoot ratio and shoot traits among rice accessions was reported [80–82].

Deep rooting has been an important trait under water stress to acquire water from deep moist soil profile to avoid drought stress [82–84]. Rice genotypes having a deep root system along with high root density and thick root system may improve the drought tolerance in upland rice [85]. Thus, the deep root system is thought to be a key factor in enhancing drought avoidance by crops [86]. Therefore, improving root system architectures in terms of root depth and high penetration in deep soil layers would be an effective strategy to avoid adverse effects of drought on yield [87]. Identified genotypes with long root system in the present study can be used as a donor in breeding rice genotypes with a long root system to confer drought tolerance. Broad sense heritability was higher for all characters studied which indicates the scope of root length improvement using diverse landraces. Phung [88] also reported high broad sense heritability for root length, root volume and root dry weight, shoot dry weight, root fresh weight, root to shoot ratio. Traits with high heritability and high genetic advance are useful to map QTLs effectively in limited marker situation.

The correlation analysis revealed that drought sensitivity score have poor correlation with many root and shoot and traits. But deep and better root system has high degree of connection to drought avoidance [19, 82–84]. The present study showed lack of correlation between root traits and drought tolerance might be due to differences in genotypes present in the study, screening technique and environment in which experiments were conducted. To find out a clear picture of the interrelationship between drought tolerance and other drought tolerance attributes, path coefficient analysis was carried out which indicated the importance of root volume and dry shoot weight and root:shoot ratio traits in improving drought tolerance in rice. These results were in consonance with the findings of Comas [14] and Kashiwagi [89] who reported that increased root biomass, root length density and rooting depth are often considered to be primary drivers of drought avoidance.

**Conclusion**

Moisture stress is the major abiotic stress affecting rice productivity in rainfed areas. Rice productivity in moisture stress prone areas of the world can be improved in sustainable ways with improvement of drought tolerance and root traits at genetic level. In the present study, 11 significant marker-trait associations were detected for various root, shoot and drought tolerance traits. Marker RM252 showed association with five traits related to shoot and root traits and RM212 showed association three root traits which suggest their scope for improvement of five traits in rice.
improvement breeding programs. The marker alleles with increasing phenotypic effects for root, shoot and drought-tolerant traits can be deployed for improvement of root, shoot and drought tolerance traits using marker-assisted selection.

References

1. Kumar, S., Dwivedi, S. K., Basu, S., Kumar, G., Mishra, J. S., Koley, T. K., Rao, K. K., Choudhary, A. K., Mondal, S., Kumar, S., Bhakta, N., Bhatt, B. P., Paul, R. K., & Kumar, A. (2020). Anatomical, agromorphological and physiological changes in rice under cumulative and stage specific drought conditions prevailed in eastern region of India. Field Crops Research, 245, 107658.

2. Yang, X., Wang, B., & Chen, L. (2019). The different influences of drought stress at the flowering stage on rice physiological traits, grain yield, and quality. Science and Reports, 9, 3742.

3. Intergovernmental Panel Climate Change (IPCC). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change 2014; Core Writing Team. In R. K. Pachauri, L. A. Meyer (Eds.) IPCC; Geneva, Switzerland, p 151.

4. Trenberth, K. E., Dai, A., Schrier, G. V. D., Jones, P. D., Barichivich, J., Griffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. Nature Climate Change, 4, 17–22.

5. Zhang, J., Zhang, S., Cheng, M., Jiang, H., Zhang, X., Peng, C., Lu, X., Zhang, M., & Jin, J. (2018). Effect of drought on agronomic traits of rice and wheat: A meta-analysis. International Journal of Environmental Research and Public Health, 15, 839.

6. Daryanto, S., Wang, L., & Jacinthe, P. A. (2017). Global synthesis of drought effects on cereal, legume, tuber and root crops production: A review. Agricultural Water Management, 179, 18–33.

7. Kim, W., Iizumi, T., Nishimori, M. (2019). Global patterns of crop production losses associated with droughts from 1983 to 2009. J Appl Meteorol Climatol, 1233–1244.

8. Kim, Y., Chung, Y. S., Lee, E., Tripathi, P., Heo, S., & Kim, K. H. (2020). Root response to drought stress in rice (Oryza sativa L.). Int J Mol Sci, 21(4), 1513.

9. Ahmadi, N., Audebert, A., Bennett, M. J., Bishopp, A., de Oliveira, A. C., Courtos, B., Diedhiou, A., Dievart, A., Gantet, P., & Ghesquière, A. (2014). The roots of future rice harvests. Rice, 7, 29.

10. Dixit, S., Singh, A., & Kumar, A. (2014). Rice breeding for high grain yield under drought: A strategic solution to a complex problem. Int J Agron, 2014, 15.

11. Palta, J. A., & Yang, J. (2014). Crop root system behaviour and yield. Field Crops Res, 165, 1–4.

12. Canales, F. J., Nagel, K. A., Müller, C., Rispaif, N., & Prats, E. (2019). Deciphering root architectural traits involved to cope with water deficit in Oat. Frontiers in Plant Science, 10, 1558.

13. Wasaya, A., Zhang, X., Fang, Q., & Yan, Z. (2018). Root phenotyping for drought tolerance: A review. Agronomy, 8(11), 241.

14. Comas, L. H., Becker, S. R., Cruz, V. M. V., Byrne, P. F., & Dierig, D. A. (2013). Root traits contributing to plant productivity under drought. Frontiers in Plant Science, 4, 442.

15. Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Haru, N., Kitomi, Y., Inukai, Y., Ono, K., & Kanno, N. (2013). Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nature Genetics, 45, 1097–1102.

16. Verma, H., Borah, J. L., & Sarma, R. N. (2019). Variability assessment for root and drought tolerance traits and genetic diversity analysis of rice germplasm using SSR markers. Science and Reports, 9, 16515.
Oryza sativaipo specie complex, wild relative of cultivated Asian rice. *Rice*, 9, 56.

35. Norton, G. J., Travis, A. J., Douglas, A., Fairley, S., De PaivaAlves, E., Ruanz-areerete, P., Naredo, M. E. B., McNally, K. L., Hossain, M., Islam, M. R., & Price, A. H. (2018). Genome wide association mapping of grain and straw biomass traits in the rice bengal and assam aus panel (BAAP) grown under alternate wetting and drying and permanently flooded irrigation. *Frontiers in Plant Science*, 9, 1223.

36. Verma, H., Devi, K. R., Baruah, A. R., & Sarma, R. N. (2020). Novel genetic resources for Magnaporthe resistance. *Frontiers in Plant Science*, 8, 1500.

37. McNally, K., Childs, K. L., Bohnert, R., Davidson, R. M., & Zhao, K. (2009). Genome wide SNP variation reveals relationships among landraces and modern varieties of rice. *Proceedings of the National Academy of Sciences*, 106, 12273–12278.

38. Yadav, S., Sandhu, N., Singh, V. K., Catolos, M., & Kumar, A. (2019). Genotyping-by-sequencing based QTL mapping for rice grain yield under reproductive stage drought stress tolerance. *Scientific reports*, 9, 14326.

39. IRRI. (2002). *Standard evaluation system for rice*. International Rice Research Institute.

40. Reynolds, S. G. (1970). The gravimetric method of soil moisture determination, Part I A study of equipments and methodological problems. *J Hydrology*, 11, 258–273.

41. Plaschke, J., Ganal, M. W., & Röder, M. S. (2005). Detection of genetic diversity in closely related bread wheat using microsatellite markers. *TAG. Theoretical and Applied Genetics.* 91, 1001–1007.

42. Panaud, O., Chen, X., McCouch, S. R. (1996). Frequency of microsatellite sequences in rice (*Oryza sativa* L.). *Genome*, 39(8), 1170–1176.

43. Sangeetha, A., Mahotra, P. K., Bhatia, V. K., & Rajendra, P. (2008). Statistical package for agricultural research (SPAR 2.0). *J Indian Soc Agric Sci*, 62, 65–74.

44. Wei, T., & Simko, V. (2017). R package “corrplot”: visualization of a Correlation Matrix (Version 0.84). https://cran.r-project.org/web/packages/corrplot/corrplot.pdf.

45. Neuwirth, E. (2014). Package ‘RColorBrewer’. https://cran.rproject.org/web/packages/RColorBrewer/RColorBrewer.pdf.

46. Bradbury, P. J., Zhang, Z., Kroon, D. E., Casstevens, T. M., Ram-doss, Y., & Buckler, E. S. (2007). TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics*, 23, 2633–2635.

47. Zhang, Z., Ersoz, E., Lai, C. Q., Todhunter, R. J., Tiwari, H. K., Gore, M. A., Bradbury, J., Yu, J., Arnett, D. K., Ordovas, J. M., & Buckler, E. (2010). Mixed linear model approach adapted for genome-wide association studies. *Nature Genetics*, 42, 355–360.

48. Rincent, R., Moreau, L., Naredo, M. E. B., Kuhn, E., Melchinger, A., Malvar, R. A., MorenoGonzalez, J., Nicolas, S., Madur, D., Combes, V., Dumas, F., Allmann, T., Brunel, D., Ouzounova, M., Flamant, P., Dubreuil, P., Charcosset, A., & MaryHuard, T. (2014). Recovering power in association mapping panels with variable levels of linkage disequilibrium. *Genetics*, 197, 375–387.

49. Das, G., Patra, J. K., & Baek, K. H. (2017). Insight into MAS: A molecular tool for development of stress resistant and quality of rice through gene stacking. *Frontiers in Plant Science*, 8, 985.

50. Balasubramanian, S., Schwartz, C., Singh, A., Warthmann, N., Kim, M. C., Maloof, J. N., Loudet, O., Trainer, G. T., Dabi, T., & Borevitz, J. O. (2009). QTL mapping in new Arabidopsis thaliana advanced intercross-recombinant inbred lines. *PLoS One*, 4(2), e4318.

51. Ibrahim, A. K., Zhang, L., Niyitanga, S., Afzal, M. Z., Zhang, L., Zhang, L., & Qi, J. (2020). Principles and approaches of association mapping in plant breeding. *Tropical Plant Biol.*, 13, 212–224.

52. Zhu, C., Gore, M., Buckler, E. S., & Yu, J. (2008). Status and prospects of association mapping in plants. *The plant genome*, 1, 5–20.

53. Pritchard, J., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155, 945–955.

54. Yu, Y., Lee, H. O., Chin, J. H., Park, H. Y., & Yoo, S. C. (2017). The complete chloroplast genome sequence of *Oryza sativa* austral type variety Nagina-22 (Poaceae). *Mitochondrial DNA Part B: Resources*, 2(2), 819–820.

55. Agrama, H. A., Eizenga, G. C., & Yan, W. (2007). Association mapping of yield and its components in rice cultivars. *Molecular Breeding*, 19, 341–356.

56. Dixit, S., Swamy, B. P. M., Vikram, P., Ahmed, H. U., Cruz, M. T. S., Amante, M., Atri, D., Leung, H., & Kumar, A. (2012). Fine mapping of QTLs for rice grain yield under drought reveals sub-QTLs conferring a response to variable drought severities. *TAG. Theoretical and Applied Genetics.*, 125, 155–169.

57. Qu, Y., Ping, M., Hongliang, Z., Chen, Y., Gao, Y., Tian, Y., Wen, F., & Li, Z. (2008). Mapping QTLs of root morphological traits at different growth stages in rice. *Genetics*, 133, 187–200.

58. Xing, Z., Tan, F., Hua, P., Sun, L., Xu, G., & Zhang, Q. (2002). Characterization of the main effects, epistatic effects and their environmental interactions of QTLs on the genetic basis of yield traits in rice. *TAG. Theoretical and Applied Genetics.*, 105, 248–257.

59. Kamoshita, A., Wade, L. J., Ali, M. L., Pathan, M. S., Zjang, J., & Sarkarung, S. (2002). Mapping QTL for root morphology of a rice population adapted to rainfed lowland conditions. *TAG. Theoretical and Applied Genetics.*, 104, 880–893.

60. Prince, S. J., Beena, R., Gomez, S. M., Sentivel, S., & Babu, R. C. (2015). Mapping consistent rice (*Oryza sativa* L.) yield QTLs under drought stress in target rainfed environments. *Rice*, 8, 25.

61. Swamy, M. B. P., Vikram, P., Dixit, S., Ahmed, H. U., & Kumar, A. (2011). Meta-analysis of grain yield QTL identified during agricultural drought in grasses showed consensus. *BMC Genomics*, 12, 319.

62. Kanagaraj, P., Prince, K. S. J., Annie Sheeba, J., Biji, K. R., Paul, S. B., Senthil, A., & Chandra Babu, R. (2010). Microsatellite markers linked to drought resistance in rice (*Oryza sativa* L.). *Cursos e Congresos da Universidade de Santiago de Compostela*, 98, 836–839.

63. Gomez, S. M., Boopathi, N. M., Kumar, S. S., Ramasubramanian, T., Chengsong, Z., Jeyaprakash, P., Senthil, A., & Babu, R. C. (2010). Molecular mapping and location of QTLs for drought-resistance traits in indica rice (*Oryza sativa* L.) lines adapted to target environments. *Acta Physiologiae Plantarum*, 32, 355–364.

64. Shao, Y. Q., Xu, J. L., Zhao, M., Laftitte, R., Zhu, L. H., Fu, B. Y., Gao, Y. M., & Li, Z. K. (2008). QTLs affecting morpho-physiological traits related to drought tolerance detected in overlapping introgression lines of rice (*Oryza sativa* L.). *Plant Science*, 174(6), 618–625.

65. Sabir, M., Shahir, G., Shah, S. M., Aslam, K., Naveed, S. A., & Arif, M. (2019). Identification and mapping of QTLs associated with drought tolerance traits in rice by a cross between Super Basmati and IR55419-04. *Breeding Science*, 69(1), 169–178.

66. Babu, R. C., Nguyen, B. D., Chamarerk, V., Shanmugasundaram, P., Chezhian, P., Jeyaprakash, P., Ganesh, S. K., Palchamy, A., Sadasivam, S., Sarkarung, S., Wade, L. J. & Nguyen, H. T. (2003). Genetic analysis of drought resistance in rice by molecular
markers: Association between secondary traits and field performance. *Crop Science*, 43, 1457–1469.
68. Salunkhe, A. S., Poornima, R., Prince, K. S., Kanagaraj, P., Sheeba, J. A., Amudha, K., Suji, K. K., Senthil, A., & Babu, R. C. (2011). Fine mapping QTLs for drought resistance traits in rice (*Oryza sativa* L.) using bulk segregant analysis. *Mol Biotechnol*, 49(1), 90–95.
69. Sandhu, N., & Kumar, A. (2017). Bridging the rice yield gaps under drought: QTLs genes and their use in breeding programs. *Agronomy*, 7(2), 27.
70. Zheng, H. G., Babu, R. C., Pathan, M. S., Ali, L., Huang, N., Courtois, B., & Nguyen, H. T. (2000). Quantitative trait loci for root-penetration ability and root thickness in rice: Comparison of genetic backgrounds. *Genome*, 43(3), 53–61.
71. Singh, S., Pradhan, S. K., Singh, A. K., & Singh, O. N. (2012). Marker validation in recombinant inbred lines and random varieties of rice for drought tolerance. *AJCS*, 6(4), 606–612.
72. Zhao, Y., Jiang, C. H., Rehman, R. M. A., Zhang, H. L., Li, J., & Li, Z. C. (2019). Genetic analysis of roots and shoots in rice seedling by association mapping. *Genes Genomics*, 41, 95–105.
73. Lanceras, J. C., Pantuwan, G., Jongdee, B., & Toojinda, T. (2004). Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiology*, 135(1), 384–399.
74. An, H., Liu, K., Wang, B., Tian, Y., Ge, Y., & Zhang, Y. (2019). Genome-wide association study identifies QTLs conferring salt tolerance in rice. *Plant Breeding*, 139, 73–82.
75. Zheng, H., Wang, J., Zhao, H., Liu, H., Sun, J., Guo, J., & Zou, D. (2015). Genetic structure, linkage disequilibrium and association mapping of salt tolerance in japonica rice germplasm at the seedling stage. *Molecular Breeding*, 35, 152.
76. Xu, F., Bao, J., He, Q., & Park, Y. J. (2016). Genome-wide association study of eating and cooking qualities in different subpopulations of rice (*Oryza sativa* L.). *BMC Genomics*, 17, 633.
77. Zhong, M., Wang, L., Yuan, J., Luo, L., Xu, C., & He, Y. Q. (2011). Identification of QTL affecting protein and amino acid contents in rice. *Rice Science*, 18(3), 187–195.
78. Guo, L., Guo, W., Zhao, H., & Wang, J. (2015). Association mapping and resistant alleles’ analysis for *japonica* rice blast resistance. *Plant Breeding*, 134, 646–652.
79. Eizenga, G. C., Jia, M. H., Jackson, A. K., Boykin, D. L., Ali, M. L., Shakiba, E., Tran, N. T., McCouch, S. R., & Edwards, J. D. (2019). Validation of yield component traits identified by genome-wide association mapping in a tropical japonica x tropical japonica rice biparental mapping population. *Plant Genome*, 12, 180021.
80. Raju, B. R., Narayanaswamy, B. R., Mohankumar, M. V., Sumanth, K. K., Rajanna, M. P., Mohanraju, B., Udayakumar, M., & Sheshshayee, M. S. (2014). Root traits and cellular level tolerance hold the key in maintaining higher spikelet fertility of rice under water limited conditions. *Functional Plant Biology*, 41(9), 930–939.
81. Courtois, B., Audebert, A., & Dardou, A. (2013). Genome-wide association mapping of root traits in a japonica rice panel. *PLoS One*, 8, e78037.
82. Henry, A., Gowda, V. R. P., Torres, R., McNally, K., & Serraj, R. (2011). Variation in root system architecture and drought response in rice (*Oryza sativa*): Phenotyping of the *Oryza* SNP panel in rainfed lowland fields. *Field Crops Research*, 120(2), 205–214.
83. Gowda, V. R. P., Henry, A., Yamauchi, A., Shashidhar, H. E., & Serraj, R. (2011). Root biology and genetic improvement for drought avoidance in rice. *Field Crops Research*, 122(1), 1–13.
84. Wasson, A. P., Richards, R. A., Chatrath, R., Misra, S. C., Prasad, S. V., & Rebetzke, G. J. (2012). Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *Journal of Experimental Botany*, 63, 3485–3498.
85. Abd Allah, A., Badawy, S. A., & Zayed, B., El-Gohary, A. (2010). The role of root system traits in the drought tolerance of rice (*Oryza sativa* L.). *World Acad Sci Eng Technol*, 68, 1378–1382.
86. Kirkegaard, J. A., Lilley, J. M., Howe, G. N., & Graham, J. M. (2007). Impact of subsoil water use on wheat yield. *Australian Journal of Agricultural Research*, 58, 303–315.
87. DeDorlodot, S., Forster, B., Pages, L., Price, A., Tuberosa, R., & Draye, X. (2007). Root system architecture: Opportunities and constraints for genetic improvement of crops. *Trends in Plant Science*, 12, 474–481.
88. Phung, N. T. P., Mai, C. D., & Hoang, G. T. (2016). Genome-wide association mapping for root traits in a panel of rice accessions from Vietnam. *BMC Plant Biology*, 16, 64.
89. Kashiwagi, J., Krishnamurthy, L., Upadhyaya, H., Krishna, H., Chandra, S., & Vadez, V. (2005). Genetic variability of drought-avoidance root traits in the mini-core germplasm collection of chickpea (*Cicer arietinum* L.). *Euphytica*, 146, 213–222.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.