Advances in configuration and genetics of crops for efficient use of water and nutrients in soil

S Song1, T Masood1,4, D M Huang1, B Wu1, Y Xu1, Y Teng2, Y Wang2, X Y Jiang3, X Q Long2,5 and F N Ma4,5
1 Haikou Experimental Station, Chinese Academy of Tropical Agricultural Sciences Hainan, 570010, China
2 Guizhou Botanic Garden, Institute of Mountain Resources of Guizhou Province, Guiyang, 550001, China
3 Research Center of Agricultural Science of Guilin, Guangxi, 541000, China
4 Department of Agricultural Chemistry, The University of Agriculture Peshawar, 25120, Pakistan.
5 E-mail: funingma@163.com, 565358995@qq.com

Abstract. As an important organ of plants, root play an important role in crop growth and development by absorbing water and nutrients from the soil. Studies on crop root systems, morphological traits, and genetic improvement of physiological functions are important in the establishment of root morphology and efficient use of water and nutrients. This paper mainly introduces the phenotypic and genetic breeding research on the efficient use of soil water and nutrients in important crops such as corn, rice, wheat, and rape. It also discusses the QTL markers and functional genes related to morphological and physiological functions and its applications in genetic improvement. Through design breeding, combined with high-throughput and high-precision root-scanning technology, screening and obtaining the ideal root structure with efficient use of soil water and nutrients, combined with techniques such as resequencing of genomes and analytical methods, the roots are selected for breeding. Crop varieties with better configuration, better quality and better yield have important promotion significance.

1. Introduction

Roots, stems, and leaves are important biological organs of crops and play an important role in growth and development. As the root system grows underground soil in the dark and the different soil substrates are difficult to separate from the root system, therefore it is difficult to observe the morphological characteristics and formation rules of the root system (main root, lateral root, and root hair) in a non-destructive state. Roots are being called the hidden half of a plant due to its importance in plant growth and also the difficulty in its study [1]. At the same time, it also limits the study of physiological functions of the root system in terms of absorption of water, macroelements, trace...
elements, and heavy metals. In recent years, with the research of imaging technology, nuclear magnetic resonance equipment with three dimensional root system function, advances in methods, rapid development of technologies applicable to field and pot phenotypic data acquisition have an important guiding significance in optimizing the root configuration and efficient use of water and nutrients in the soil [2]. In recent years, there have been many researches described the relationship between crop root structure and its efficient use of water and nutrients, including root morphological traits and genetic characteristics of their associated genes, related to root nitrogen, phosphorus, potassium, iron, and water absorption. Great progress has been made in the localization, cloning and functional research of related physiological functions of genes.

The evaluation of different feature of root system architecture and its use in breeding program is limited due to difficulty in phenotyping root traits in the field [3]. Techniques applied in the field are more labor taking and need plot damage for sample collection. The variation in the soil structure and composition that influences the RSA of field crops at different locations within a same field is another factor. The RSA of field crops at different locations within a same field can be affected by variation in soil structure and composition. This is another factor confusing the effect due to genetic and environmental interactions.

Despite such difficulties, through the use of innovative technologies, researchers have developed some high-throughput root phenotyping detection techniques and analysis technologies [4] [5]. The most popular in recent years is the gel-based root culture analysis technology [6] [7]. The machine is combined with high-definition camera captures the growth status of the root system and then analyses the imaging system to obtain the whole root system or analysis of the spatiotemporal changes in the growth and elongation of a certain part of the plant [8] [9].

Physiological irrelevance may be present due to gel-based root analysis which is providing visual access to the roots for non-destructive imaging. These root growth systems can be used for analyzing large number of individuals or genotypes under controlled environmental conditions in order to get the reproducible results. More physiologically relevant data would be provided by the no-destructive imaging of roots in soil filled container which still allow to test the specific environmental condition. However there is limitation in throughput and the spatial resolution with the soil based root imaging methods [10].

In recent years, X-ray scanning technology and nuclear magnetic resonance imaging root system are used for phenotypic detection. The above techniques have their own advantages and disadvantages, such as X-ray scanning technology is easily affected by water and organic matter by weakening the signal strength at the root [8] [11]. While comparing the two technologies, NMR technology can detect more root systems than X-rays. Line scan technology can get more root detailed imaging and get faster and more accurate roots phenotypic analysis data [4] [12]. The establishment of a three-dimensional root structure model functions for studying the absorption and utilization of water and nutrients in crop roots. It has a good effect and researchers such as Lynch proposed the Sim Root simulation and Visualization system to simulate root growth dynamics and nutrient uptake [13].

In recent years the popular Smart Root online software system [13] [14] [15], including the relatively new Root Nav 2.0 version, Quality image analysis [16].

2. Genetic characteristics of crop roots and their use in breeding

2.1. Quality Trait Loci (QTLs) for root morphological traits and physiological functions and their use in breeding

There is a complex gene system for controlling the morphological traits and root architecture. Several genes operate in the complex gene system to produce a desired phenotype. Root genetics study
becomes difficult due to root responses and multiple gene control traits. Also, large number of plants are required to study the root genetics in the soil and field experiments which is the most valid phenotypic evaluation.

The genetic traits of the root system are mainly quantitative traits. The method of association analysis quality trait locus (QTL) mapping is used. Many research methods have been reported in recent years in rice, rape, corn, wheat, and other crops. There are many QTL studies relates the root traits and physiological functions of rice, mainly combined with detection of root phenotype analysis and obtained a batch of direct phenotypes such as root length, root area, lateral root number, indefinite root number, and root vitality QTL of the data [6] [2]. It plays an important role in assisting breeding in these crops. Rice root related traits are mainly distributed on chromosomes 1, 2, 5, 9, and 11. There is a QTL that controls root surface area, number, and root length on chromosome 11 [17]. The traits related to water stress are mainly located on chromosomes 2, 3, 5, 6 and 9. It was found that there was a linkage between root traits and cold resistance and yield traits at seedling stage [18]. Mapping of root length QTLs on chromosome 4 in rice backcross populations using transparent agar root culture analysis in the range of 624.6 kb [7].

With the maturity and widespread application of genome sequencing technology, Liu et al. [19] determined efficient nitrogen use QTLs and found that the two QTLs RM5639 and RM3628 each contain known nitrogen utilization efficiency related genes GS1; 2 and AspAt3, and a new QTL locus RM5748 for nitrogen use efficiency in rice [19]. Pang et al. [20] through simultaneous mapping using the breeding population selection and gene sequencing technology identified three QTLs affecting salt damage score and leaf chlorophyll content. These three QTLs were located on chromosomes 1, 2, and 4 respectively. Through SNP data and genotype analysis, 87 salt-tolerant QTLs and candidate genes were obtained [20]. QTL pyramiding method may be a joint improvement of crop traits and genetic analysis.

2.2. Effective strategies for the separation.

Some advances have been made in QTL genetic analysis of morphological and nitrogen efficiency traits in maize. Eight seedling root traits were detected at three different development stages after seed germination, and a total of 36 were detected. QTLs explaining 9.0-23.2% of the phenotypic variation range of root traits, these QTLs are distributed across 10 stains physically, at least 5 QTLs are distributed on chromosomes 1, 5, and 8 at different stages of development. Root traits of maize seedlings are regulated by different pleiotropic QTLs [6].

Liu et al. [21] identified 14, 18 and 14 QTLs of RSA and the phenotype of these QTLs was evaluated in maize seedlings under three root growth systems of different substrates such as paper rolls, hydroponics, and vermiculite respectively. Correlation was determined between RSA traits with nitrogen and phosphorus uptake efficiency traits in maize inbred line young seedlings under field conditions. Phenotypic associations were observed for most of RSA traits among all three culture systems. Hydroponic or vermiculite proved to be better than paper roll method for assessing the RSA traits at seedling stage and it is important index to accelerate the screening of high-uptake nitrogen and phosphorus genotypes for maize breeding programs.

In rapeseed, the location and utilization of QTL have also made good contribution in the nutrient use efficiency. Genetic analysis of root morphological traits related to potassium use efficiency in rapeseed using hydroponic technology was found useful. Under the conditions of high and low potassium, and high and low nitrogen, 5 major QTL clusters were detected. Four clusters were specifically detected under the low potassium and low nitrogen conditions. These common and specific QTLs may help improve multiple traits simultaneously with marker-assisted selection [22] [23]. 4 QTLs and 20 QTLs were associated with root morphological traits at high and low nitrogen levels respectively [24]. Xie et al. [2] identified the relationship between root structure characteristics and yield and yield components of wheat seedlings. There are 38 QTLs between root structure traits and yield and yield components of wheat seedlings. The QTL overlap rate is high, indicating that there is a tight linkage or Pluripotency, consistent with phenotypic correlation analysis results [2].
2.3. Nitrogen and phosphorus

Good results have been achieved by studying QTL mapping of phosphorus use efficiency and agronomic traits. There have been 121 and 130 QTLs detected at different nitrogen levels, 47 relatively high-frequency QTLs, and 16 QTL cluster. Most important cluster is C9 which covers root morphology, biomass, yield and absorption and utilization efficiency traits. 17 high-frequency QTLs were detected in C9. By comparing genomes, it was found that C9 utilization efficiency was related to D3940950. The marker is 100% similar to the RhtB1 gene and the results can be used for large-scale recognition of major indicators of absorption and utilization efficiency of nitrogen [25].

Marker assisted selection in wheat breeding for phosphorus utilization efficiency, four important QTL clusters and 11 high frequency QTL were discovered in wheat. Four QTLs clusters were found to have favorable relationships for breeding programs giving the chance of improvement in morphological traits and phosphorus utilization efficiency at the same time. Homologous association with EST was found among 29 markers and 51 QTLs suggesting to be potential loci. The main index for Phosphorus absorption and utilization were suggested to be four biomass traits (SDW, RD, TDW and RSDW), five yield traits (SN, PH, TGW, GWP and StWp) and two relative traits (RsTwp and Rgwp) [26].

These common and specific root morphological traits, nitrogen and phosphorus use efficiency, water uptake and stress related main effects QTL, cluster QTL, one-factor multiple effect QTL, etc., can be used as crop root-related heredity. An important basis for breeding trait molecules, speeding up gene mapping and cloning of important root traits or physiological functional traits and molecular breeding processes, while also helping to improve multiple traits at the same time through marker-assisted breeding. The goal of high-quality and efficient breeding. In addition, with modern molecular biology, especially genome sequencing, development of various omics, and the development of new genetic populations such as near-isogenic lines and chromosome fragment substitution lines Developed a QTL mapping clone from the traditional QTL mapping, gradually transitioned to almost complete quality traits Identical location clones also reduce the traditional QTL-assisted breeding Effect QTL contains missing important genes.

2.4. Genes of root morphological traits and physiological functions and their use in breeding

With rapid development of genomics, the basis of crops through mutant cloning and population construction. Many regulated root lengths, lateral roots, Genes of traits such as adventitious roots, root tips, root hairs, etc. Functional genes such as quantitative elements, water use, and root involvement in stress resistance were gradually identified [23] [6]. Its comprehensive utilization with traditional breeding technology, etc. the improvement of efficiency and effect is of great significance. These genes related to root architecture and physiological functions also involves many physiological and biochemical metabolic pathways, including plant important homones, such as auxin, cellular Lysin, etc., and some pathways related to biotic and abiotic stress signals [24].

In recent years, more genes about the function of root system have been reported in rice. In response to external low concentration of phosphate, OsAUX1 transgenic rice can promote root hair elongation. This study demonstrates that OsAUX1 has function to transport auxin from the root tip to the differentiation zone. External low-phosphorus conditions can promote root hair elongation, so auxin plays a key role in promoting the development of rice roots [27]. Rice OsPIN2 regulate root growth and lateral root development by regulation of auxin distribution in the root tip region [28]. Os4BGlu10, Os6BGlu24 and Os9BGlu33 in rice play an important role in root elongation of plants. Mutants bglu10, bglu24 and bglu33 longer roots compared to the wild type. All the mutants showed lower tolerance to drought and survival rate was significantly reduced. The reduction in relative leaf water content and Fv / Fm ratio after treatment was confirmed [29].

Novel rice (Oryza sativa) DOF transcription factor OsDOF15 regulates cell proliferation in root meristem by limiting ethylene biosynthesis actively regulate primary root elongation. Loss of function of OsDOF15 can damage primary root elongation and cell proliferation in the root meristems, and overexpression of OsDOF15 enhances these processes, suggesting that OsDOF15 is the key regulator
of primary root elongation. OsDOF15's control of ethylene biosynthesis in turn regulates cell proliferation in root meristems. Salt stress inhibits OsDOF15 transcription and OsDOF15-mediated ethylene biosynthesis plays a role in inhibiting primary root elongation under salt stress [30]. The transcription factor OsERF71 is known to change the structure of root system in rice and improve its drought resistance. Overexpression of OsERF71, whether in the entire plant or in the roots, especially during the vegetative stage, can lead to drought resistance phenotype. At the reproductive stage, root-specific overexpression was more effective in conferring drought resistance. Under drought conditions, grain yield was increased by 23% to 42% over wild-type plants. Overexpression of OsERF71 in roots increases the expression level of genes related to cell wall relaxation and lignin biosynthetic genes, which is correlated to changes in root structure, formation of enlarged aerenchyma and high levels of lignification [31].

In corn plant, the expression level of aquaporin genes ZmPIP2; 2, ZmPIP2;6 and ZmTIP2;2 increased due to the presence of Yb3+ earth metal. Thus proving that overall membrane permeability can be increased by regulating the expression of aquaporin genes responsible for transmembrane water transport in corn roots [32]. It is considered that a maize AP2/ERF transcription factor, ZmRAP2.7, is involved in brace roots development. ZmRAP2.7 expressed in all types of roots. A maize transposon s mutant RAP2.7-Mu defective in ZmRAP2.7 expression revealed a decreased number of brace roots but not crown roots revealing corn RAP2.7 transcription factors can regulate maize root development. Abscisic acid regulates auxin distribution to regulate lateral root development of maize under salt stress [33].

A gene designated with a name as ZmPP2AA1 (*Zea mays* L. protein phosphatase 2A regulatory subunit A) was introduced in the roots of Maize plant with low available inorganic phosphate (Pi) level in soil. RNA interference and overexpression analysis were used to know the function of ZmPP2AA1 maize plant. ZmPP2AA1 is involved in the stimulation of lateral roots development while negatively regulate the growth of primary roots. It is also responsible for the modulation of root gravitropism. It was known that auxin has the contribution in root system response (RSA) response to low availability of Pi after thorough examination of RSA to different concentration of Pi with or without IAA and 1-N-naphthylphthalamic acid. Transgenic maize in hydroponic as well as in soil conditions showed elevated response to Pi deficiency due to overexpression of ZmPP2AA1. Increased dry weight, root to shoot ratio and total P content in overexpressed transgenic maize plants were coincided with its highly branched root system and increased Pi uptake efficiency under low Pi conditions. ZmPP2AA1 overexpressed maize line was resulted in higher grain yield per plant under low Pi level due to less effects on it inflorescence development during Pi starvation [34].

In rape, Xie et al. found that Abscisic acid (ABA) regulates the effects of graphite oxide which is an important factor affecting the growth and development of *Brassica napus*. These treatments significantly increased the concentrations of ABA and gibberellin in the rape seedlings by affecting the transcriptional level of major genes involved in the ABA, Indole acetic acid, cytokinin, salicylic acid and ethane pathways. The treatment suppressed the root elongation however the effects of the treatments on the IAA and CTK contents were complex [35]. In hexaploid wheat, brassinosteroids regulate the development of their roots through highly redundant genes [36].

2.5. Water shortage

Comparing transgenic and wild type wheat plants by competitive growth analysis under water limited conditions, it was observed that in transgenic wheat line TaNAC69-1 with OsPRSP3 promoter-driven produced 35 and 32% more grains and above ground biomass respectively than wild type. Expression of TaSHY2 and TaIAA7 from the Auxin transcriptional gene family and are homologs of SHY2/IAA3 and IAA7 which are negative root growth regulators in Arabidopsis were down regulated due to the overexpression of TaNAC69-1 gene responsible for the root growth at early growth stage in wheat. Drought stress made the expression of TaSHY2 and TaIAA7 genes down regulated while it was up-regulated by cytokinin treatment which is a root growth suppressor. TaNAC69-1 bound to the promoters of TaSHY2 and TaIAA7, acting as a transcriptional repressor and repressed the expression
of reporter genes driven by the TaSHY2 or TaIAA7 promoter as evident from the DNA binding and transient expression analysis. These results suggest that TaNAC69-1 is likely to be responsible in the root elongation in drying soil conditions by acting as transcriptional repressor of TaSHY2 and TaIAA7 which are homologous to negative growth regulators of Arabidopsis [37].

2.6. Analysis on the utilization trend of root system configuration in breeding

Root growth and development and adaptability to the soil environment are important parts of healthy crop growth. The development of root system phenotypic technology is crucial. Rapid development of high-throughput root phenotypic technologies in recent years, including scanning integrated technology such as imaging technology, MRI technology, Root Type model, smart Root software system, etc. gradually optimized and utilized in the better achievement of the root structure, dynamic growth process, absorption and utilization of nutrients etc. laid the foundation for phenotypic observation of species resistance to environmental stress in the soil [14] [15]. Therefore, the root system research technology, the optimal design of root system configuration and breeding research System configuration to achieve better water use and nutrient absorption, resistance to various stresses, etc. is of great significance.

Root system research techniques and phenotypic detection and analysis of root system configuration are the most direct evidence to obtain crop root characteristics. In the breeding research aimed at the establishment of the root system and the optimization design of the root system, Population construction, hybrid breeding, and genome sequencing assisted breeding to screen the dominant root configuration of crops. At the same time, it can assist in the relative systematic analysis and detection of nutrients, water absorption and utilization by the crops in the soil. Efficiency, a relatively clear description of the relationship between root architecture, physiological functions, and environmental adaptation, which is important for modern breeding. The development of technology and the acceleration of the directed breeding process have greatly promoted [38]. However, the current scan imaging technology is mainly used for indoor and pot experiments, and it is not yet possible to achieve full field varieties research and utilization in breeding.

It is concluded that in the field of genetic research of root structure and efficient use of soil moisture and nutrients by crops, the development of root phenotyping technology is the foundation. The use of high-throughput and high-precision root scanning technology can make root structure more intuitive and accurate. Through the design of breeding and screening and root system configurations combined with genomic sequencing made the plants efficient in using water and nutrients from the soil. It has an important significance for breeding crop varieties with better root structure and better quality and yield [39].

Acknowledgement

This research was funded by the Foundation of Hainan Province of China [grant number ZDYF2019090] and the Foundation of Guizhou Province of China [grant number 20192269, 20194005].

References

[1] Waisel Y, Eshel A, Beeckman T and Kafkaki U 2005 Plant roots: The hidden half 1st edn. (New York).
[2] Xie Q, Fernando K M C, Mayes S and Sparkes D L 2017 Identifying seedling root architectural traits associated with yield and yield components in wheat Ann. Bot. 119 1115-29.
[3] Richards R A 2008 Genetic opportunities to improve cereal root systems for dryland agriculture Plant Prod. Sci.11 12-6.
[4] Soltaninejad M, Sturrock C, Griffiths M, Pridmore T and Pound M 2020 Three dimensional root CT segmentation using multi-resolution encoder-decoder networks IEEE Trans. Image Process.29 6667-79.
[5] Thomas C L, Graham N S, Hayden R, Meacham M C, Neugebauer K, Nightingale M, Dupuy L
X, Hammond J P, White P J and Broadley M R 2016 High-throughput phenotyping (HTP) identifies seedling root traits linked to variation in seed yield and nutrient capture in field-grown oilseed rape (Brassica napus L.) *Ann. Bot.* **118** 655-65.

[6] Ju C, Zhang W, Liu Y, Gao Y, Wang X, Yan J, Yang X and Li J 2018 Genetic analysis of seedling root traits reveals the association of root trait with other agronomic traits in maize *BMC Plant Biol.* **18** 171.

[7] Xu X M, Zhang Y X, Wang H M, Ren C and Cao L Y 2016 Identification qRL4, a major quantitative trait locus associated with rice root length *Chin. J. Rice Sci.* **30** 363-70.

[8] Meeinkuirt W, Phusantisampam T and Saengwilai P 2019 Root system architecture influencing cadmium accumulation in rice (Oryza sativa L.) *Int. J. Phytoremediation* **21** 19-26.

[9] Uga Y, Assaranurak I, Kitomi Y, Larson B G, Craft E J, Shaff J E, McCouch S R and Kochian L V. 2018 Genomic regions responsible for seminal and crown root lengths identified by 2D & 3D root system image analysis *BMC Genom.* **19** 273.

[10] Mairhofer S, Zappala S, Tracy S R, Sturrock C, Bennett M, Mooney S J and Pridmore T 2012 RooTrak: Automated recovery of three-dimensional plant root architecture in soil from X-Ray microcomputed tomography images using visual tracking *Plant Physiol.* **158** 561-69.

[11] Saengwilai P, Meeinkuirt W, Phusantisampam T and Pichtel J 2020 Immobilization of cadmium in contaminated soil using organic amendments and its effects on rice growth performance *Exp. Heal.* **12** 295-306.

[12] Chen X, He R, Ding Q and Sun Q 2019 A Digitization and visualization procedure for 3D wheat root system architecture in rice–wheat rotation *J. Inst. Eng. Ser. A* **100** 1-8.

[13] Lynch J P, Nielsen K L, Davis R D and Jablokow A G 1997 SimRoot: Modelling and visualization of root systems *Plant Soil* **188** 139-51.

[14] Wu J, Wu Q, Pagès L, Yuan Y, Zhang X, Du M, Tian X and Li Z 2018 RhizoChamber-Monitor: A robotic platform and software enabling characterization of root growth *Plant Methods* **14** 44.

[15] Lobet G, Pagès L and Draye X 2011 A novel image-analysis toolbox enabling quantitative analysis of root system architecture *Plant Physiol.* **157** 29-39.

[16] Yasrab R, Atkinson J A, Wells D M, French A P, Pridmore T P and Pound M P 2019 RootNav 2.0: Deep learning for automatic navigation of complex plant root architectures *Gigascience* **18** 1-16.

[17] Shukun J, Zhang F, Bai L, Sun S, Wang T, Ding G J H and Zhang X 2014 QTL analysis on new root traits after rice transplantation *Chin. J. Rice Sci.* **28** 598-604.

[18] Rongrong Z et al. 2012 QTL mapping for root traits in rice seedlings under different water supply conditions *J. Nucl. Agri. Sci.* **26** 975-82.

[19] Liu Z et al. 2016 Association mapping and genetic dissection of nitrogen use efficiency-related traits in rice (Oryza sativa L.) *Funct. Integr. Genomics* **16** 323-33.

[20] Pang Y, Chen K, Wang X, Wang W, Xu J, Ali J and Li Z 2017 Simultaneous improvement and genetic dissection of salt tolerance of rice (Oryza sativa L.) by designed QTL pyramiding *Front. Plant Sci.* **8** 1275.

[21] Liu Z, Gao K, Shan S, Gu R, Wang Z, Craft E J, Mi G, Yuan L and Chen F 2017 Comparative analysis of root traits and the associated QTLs for maize seedlings grown in paper roll, hydroponics and vermiculite culture system *Front. Plant Sci.* **8** 436.

[22] Dun X, Shi J, Liu H, Wang J, Wang X and Wang H 2019 Genetic dissection of root morphological traits as related to potassium use efficiency in rapeseed under two contrasting potassium levels by hydroponics *Sci. China Life Sci.* **6** 746-57.

[23] Wang X et al. 2017 Genetic variants associated with the root system architecture of oilseed rape (Brassica napus L.) under contrasting phosphate supply *DNA Res.* **24** 407-17.

[24] Wang J, Dun X, Shi J, Wang X, Liu G and Wang H 2017 Genetic dissection of root morphological traits related to nitrogen use efficiency in brassica napus L. Under two contrasting nitrogen conditions *Front. Plant Sci.* **8** 1709.
[25] Zhang M et al. 2019 QTL mapping for nitrogen use efficiency and agronomic traits at the seedling and maturity stages in wheat Mol. Breed. 39 71.

[26] Yuan Y, Gao M, Zhang M, Zheng H, Zhou X, Guo Y, Zhao Y, Kong F and Li S 2017 QTL mapping for phosphorus efficiency and morphological traits at seedling and maturity stages in wheat Front. Plant Sci. 8 614.

[27] Giri J et al. 2018 Rice auxin influx carrier OsAUX1 facilitates root hair elongation in response to low external phosphate Nat. Commun. 9 1810.

[28] Inahashi H, Shelley I J, Yamauchi T, Nishiuchi S, Takahashi-Nosaka M, Matsunami M, Ogawa A, Noda Y and Inukai Y 2018 OsPIN2, which encodes a member of the auxin efflux carrier proteins, is involved in root elongation growth and lateral root formation patterns via the regulation of auxin distribution in rice Physiol. Plant. 164 216-25.

[29] Ren R, Li D, Zhen C, Chen D and Chen X 2019 Specific roles of Os4BGlul0, Os6BGluc24, and Os9BGluc33 in seed germination, root elongation, and drought tolerance in rice Planta 249 1851-61.

[30] Qin H et al. 2019 Rice OsDOF15 contributes to ethylene-inhibited primary root elongation under salt stress New Phytol. 223 798-813.

[31] Lee D K, Jung H, Jang G, Jeong J S, Kim Y S, Ha S H, Choi Y Do and Kim J K 2016 Overexpression of the OsERF71 transcription factor alters rice root structure and drought resistance Plant Physiol. 172 575-88.

[32] Vorob’ev V N, Sibgatullin T A, Sterkhova K A, Alexandrov E A, Gogolev Y V., Timofeeva O A, Gorskov V Y and Chevela V V. 2019 Ytterbium increases transmembrane water transport in Zea mays roots via aquaporin modulation BioMetals 32 901-8.

[33] Li J, Chen F, Li Y, Li P, Wang Y, Mi G and Yuan L 2019 ZmRAP2.7, an AP2 transcription factor, is involved in maize brace roots development Front. Plant Sci. 10 820.

[34] Wang J, Pei L, Jin Z, Zhang K and Zhang J 2017 Overexpression of the protein phosphatase 2A regulatory subunit a gene ZmPP2AA1 improves low phosphate tolerance by remodeling the root system architecture of maize PLoS One 12 e0176538.

[35] Xie L L, Chen F, Zou X L, Shen S S, Wang X G, Yao G X and Xu B B 2019 Graphene oxide and ABA cotreatment regulates root growth of Brassica napus L. by regulating IAA/ABA J. Plant Physiol. 240 153007.

[36] Hou L, Zhang A, Wang R, Zhao P, Zhang D, Jiang Y, Diddugodage C J, Wang X, Ni Z and Xu S 2019 Brassinosteroid regulates root development with highly redundant genes in hexaploid wheat Plant Cell Physiol. 60 1761-77.

[37] Chen D, Richardson T, Chai S, McIntyre C L, Rae A L and Xue G P 2016 Drought-up-regulated TaNAC69-1 is a transcriptional repressor of TaSHY2 and TaLAA7, and enhances root length and biomass in wheat Plant Cell Physiol. 57 2076-90.

[38] Chocois V, Voge J P, Rebetzke G J and Watt M 2015 Variation in adult plant phenotypes and partitioning among seed and stem-borne roots across Brachypodium distachyon accessions to exploit in breeding cereals for well-watered and drought environments Plant Physiol. 168 953-67.

[39] Shilin D L C and Qian Q 2019 Research progress on genetic of rice root China Rice 25 24-9.