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Invited Review

Transcriptome-based approaches for clarification of nutritional responses and improvement of crop production

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Genome-wide transcriptome profiling is a powerful tool for identifying key genes and pathways involved in plant development and physiological processes. This review summarizes studies that have used transcriptome profiling mainly in rice to focus on responses to macronutrients such as nitrogen, phosphorus and potassium, and spatio-temporal root profiling in relation to the regulation of root system architecture as well as nutrient uptake and transport. We also discuss strategies based on meta- and co-expression analyses with different attributed transcriptome data, which can be used for investigating the regulatory mechanisms and dynamics of nutritional responses and adaptation, and speculate on further advances in transcriptome profiling that could have potential application to crop breeding and cultivation.

Key Words: transcriptome profiling, nutritional response, rice, root, field.

Introduction

As latest estimates suggest that the world human population will have increased by 2 billion by 2050, innovative solutions will be required for improvement of agricultural food productivity. Rice is a major cereal crop that is the staple food for almost half of the world's population. To ensure food security for the growing world population, it will be necessary for rice yield to approximately double in the next 30 years (Ray *et al.* 2013). Plants require 17 essential elements, of which nitrogen (N), phosphorus (P) and potassium (K) are applied to rice fields as chemical fertilizers in large quantities. As well as having marked effects on crop yield, this also creates various issues related to agricultural management and the natural environment. Most of N fertilizers are released into the air, water or soil, creating severe environmental pollution because approximately 20% of the applied N fertilizer is taken up by the rice plant (Ju *et al.* 2009). Since most of the P existing naturally in soil is in the form of organic compounds or sparingly soluble cationic complexes, phosphate (Pi), an inorganic form of phosphorus available for plants, is a limiting factor for crop production in more than 50% of the world's cultivable soils (Lynch 2011). In addition, approximately 20% of the applied Pi is absorbed by plants, and then the remainder forms insoluble organic complexes, thereby causing pollution to environment as in the case of N (Vance *et al.* 2003). Although K is the fourth most abundant mineral element on earth (Sparks and Huang 1985), only free K ions can be absorbed and utilized by plants, and the concentration of free K in the soil is usually below 1 mM (Luan *et al.* 2009).

Plants absorb nutrients from soil and then translocate them to various organs. To maintain this process, plants have a high adaptability to the nutritional environment in the rhizosphere and exhibit various physiological and morphological responses such as modulation of the root system architecture (RSA) and regulation of nutrient absorption and transport processes. Therefore, in order to develop new rice varieties with better nutrient use efficiency and tolerance to unfavorable nutrient conditions, it is necessary to understand the molecular mechanisms involved in response and adaptation to nutritional environments, allowing sustainable optimization of crop production and reduction of environmental impacts. Genome-wide transcriptome analysis is a powerful approach for clarifying these molecular aspects and providing information on the regulatory networks that control plant nutrient acquisition and usage. In an attempt to identify genes that are responsive to nutrient conditions in terms of N, P and K, a number of studies involving comprehensive transcriptome analysis of various plant species, including rice, have been reported (rice: **Table 1**, others: Armengaud *et al.* 2004, Canales *et al.* 2014, Gelli *et al.* 2014, Hammond *et al.* 2003, Hao *et al.* 2011, Krapp *et al.* 2011, Misson *et al.* 2005, Nilsson *et al.* 2010, Wang *et al.* 2000, 2003, Woo *et al.* 2012).

Response to nitrogen

N is needed in large amounts for plants to grow and is a

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Table 1. Transcriptome profiling in response to varied nutrient conditions in rice

Nutrient[a]	Treatment[a]	Nutrient form	Treatment period[a]	Tissue[a]	Stage[a]	Cultivar[b]	Tool[a]	Reference[a]
N	–N	NH_4NO_3	1 h, 24 h, 7 d	root, shoot	five-leaf stage	Hejiang 19 (J)	microarray	Cai *et al.* 2012
	+N	$(NH_4)2SO_4$	3 h	root	17 day seedling	Dongjin (J)	microarray	Chandran *et al.* 2016
	–N	NH_4NO_3	1 h	root	10 day seedling	TNG67 (J)	microarray	Hsieh *et al.* 2018
	Low N	NH_4NO_3	20 min, 1, 2 h	root, shoot	four-leaf stage	Minghui 63 (I)	microarray	Lian *et al.* 2006
	Low N	NH_4NO_3	15 d	root, shoot	15 day seedling	IR64 (I), Nagina 22 (I)	RNA-seq	Sinha *et al.* 2018
	Low N, High N	NH_4NO_3	30 d	root	three-leaf stage	Shennong265 (J)	RNA-seq	Xin *et al.* 2019a
	Low N, High N	NH_4NO_3	30 d	leaf	three-leaf stage	Shennong265 (J)	RNA-seq	Xin *et al.* 2019b
	–N, HighN	$(NH_4)2SO_4$	4 h	root, shoot	10 day seedling	Nipponbare (J)	RNA-seq	Yang *et al.* 2015a
	Low N	NH_4NO_3	12 h	root, leaf sheah	six-leaf stage	Dongjin (J)	RNA-seq	Yang *et al.* 2015b
	–N	NH_4NO_3	30 min	root	17 day seedling	TNG67(J)	microarry	Yang *et al.* 2017
P	Low P	NaH_2PO_4	6, 24 h, 2, 3 d	seedling	7 day seedling	Zhonghua 10 (J)	microarray	Dai *et al.* 2012
	Low P	NaH_2PO_4	9 d	leaf root	15 day seedling	Dongxiang (W)	RNA-seq	Deng *et al.* 2018
	Low P	NaH_2PO_4	6, 24 h, 3 d	root	four-leaf stage	Zhongzao18 (I), Lagrue (I)	microarray	Li *et al.* 2010
	Low P	NaH_2PO_4	15 d	root, shoot	2 day seedling	Dular (I), PB1(I)	microarray	Mehra *et al.* 2016
	Low P	NaH_2PO_4	10, 22d	root, shoot	14 day seedling	Nipponbare (J), IAC 25 (J) Vary Lava 701 (J) Kasalath (I)	RNA-seq	Oono *et al.* 2013
	pot with –P field soil		40 d	root, shoot	seed	Nipponbare (J), NIL (*Pup1*)	microarray	Pariasca-Tanaka *et al.* 2009
	Low P	NaH_2PO_4	5 d	leaf	three-leaf stage	Dongjin byeo (J)	microarray	Park *et al.* 2012
	–P, +P	NaH_2PO_4	1, 6, 24 h, 3, 7 d, 21 d (–P) 1, 6, 24 h (+P)	root, shoot	14 day seedling	Nipponbare (J)	RNA-seq	Secco *et al.* 2013
	Low P	NaH_2PO_4	15 d	root	15 day seedling	Sahbhagi Dhan (I) Chakhao Poreiton (I)	RNA-seq	Tyagi and Rai 2017
	–P	NaH_2PO_4	1, 9 d	root	7 day seedling	Michikogane (J)	microarray	Wasaki *et al.* 2003
	–P	NaH_2PO_4	1, 9 d	leaf	7 day seedling	Michikogane (J)	microarray	Wasaki *et al.* 2006
K	–K	K_2SO_4	6 h, 3, 5 d	root	14 day seedling	Nipponbare (J)	microarray	Ma *et al.* 2012
	Low K	K_2SO_4	24 h, 2, 4 d	root	three-leaf stage	Nipponbare (J)	RNA-seq	Zhang *et al.* 2017
NPK	–N, –P, –K	NH_4NO_3, NaH_2PO_4, K_2SO_4	6, 24 h	root	7 day seedling	Nipponbare (J)	microarray	Takehisa *et al.* 2013
	Low N, P, K	NH_4NO_3, NaH_2PO_4, K_2SO_4	5 d	shoot	7 day seedling	Nipponbare (J)	microarray	Takehisa *et al.* 2015
	High N, P, K	NH_4NO_3, NaH_2PO_4, K_2SO_4	5 d	shoot	7 day seedling	Nipponbare (J)	microarray	Takehisa and Sato 2019

[a] –N: N-free, –P: P-free, –K: K-free, +N; recovary N after deficiency, +P; recovary P after deficiency.
[b] J: *japonica*, I: *indica*, W: wild rice.

constituent of cellular molecules such as adenosine triphosphate (ATP), amino acids, nucleic acids, and chlorophyll. Thus, N deficiency affects all fundamental aspects of plant growth and development, and causes leaf chlorosis, modulation of the RSA and reduced yield. Generally, mild N deficiency lead to an increase of root growth, while root growth is inhibited in cases of excess supply of N and severe N deficiency (Giehl and Wirén 2014). In rice, it has also been reported that root length and biomass are increased and shoot biomass is decreased under low N, and that high N conditions promote shoot growth and suppress root growth, respectively (Hsieh *et al.* 2018, Sinha *et al.* 2018, Sun *et al.* 2016, Xin *et al.* 2019a, 2019b). The complex and diverse morphological and physiological changes induced by N starvation suggest that response and adaptation to N deficiency involve multiple signaling and metabolic pathways. Whole-genome transcriptome analyses of rice shoots and/or roots derived from seedling plants grown under various N conditions, i.e., N-free (–N), low N, high N and recovery of N after deficiency (+N), has been conducted (**Table 1**).

N absorption, assimilation and remobilization

Many previous studies in this field have been conducted using mainly *Arabidopsis*, and this has led to clarification of the genes and molecular mechanisms involved in the absorption, distribution, and assimilation of N (Wang *et al.* 2018b, Xuan *et al.* 2017). In rice, the key components such as nitrate transporter genes (*NRTs*/*NPFs*) and ammonium transporters genes (*AMTs*) have now been identified and characterized. OsNPF8.9 (OsNRT1.1), OsNPF6.5 (OsNRT1.1B), OsNRT1.1b, OsNPF2.4 (OsNRT1.6), OsNRT2.1, OsNRT2.2, OsNRT2.3a, OsNRT2.3b, OsNRT2.4 and OsNPF2.2 play a role in uptake in the rhizosphere and/or translocation of NO_3^- (Fan *et al.* 2015, Feng *et al.* 2011, Hu *et al.* 2015, Li *et al.* 2015, Lin *et al.* 2000, Tang *et al.* 2012, Wang *et al.* 2018a, Xia *et al.* 2015, Yan *et al.* 2011). On the other hand, it has been proposed that the ammonium transporters (AMTs), OsAMT1, OsAMT2, and OsAMT3, function in the absorption of NH_4^+ (Sonoda *et al.* 2003, Suenaga *et al.* 2003). Absorbed NO_3^- is converted by the nitrate reductase (NR) and the nitrite reductase (NiR) to NH_3 and then NH_3 feeds into the GS/GOGAT cycle of amino acid biosynthesis. In the assimilation, the cytosolic glutamine synthetase genes, i.e., *GS1;1*, *GS1;2*, and *GS1;3*, and the NADH-glutamate synthase genes, i.e., *NADH-GOGAT1* and *NADH-GOGAT2*, have been identified in rice (Tabuchi *et al.* 2005, Tamura *et al.* 2010, 2011), and their encoded isoenzymes are thought to have distinct and non-overlapping functions; *OsGS1;2* and *OsNADH-GOGAT1* are expressed mainly in root surface cells and the expression of *OsGS1;1* and *OsNADH-GOGAT2* has been observed mainly in the vascular tissues of mature leaf blades (Tabuchi *et al.* 2007). Remobilization of nitrogen from senescent leaves is closely related to nutrient use efficiency. Autophagy is an evolutionarily conserved degradation system for intracellular components in eukaryotic cells (Nakatogawa *et al.* 2009) and its machinery has been demonstrated to contribute nitrogen remobilization in *Arabidopsis* and rice (Guiboileau *et al.* 2012, Wada *et al.* 2015).

Expression dynamics of the genes responsive to N conditions

Yang *et al.* (2015a) identified 862 genes (394 in roots/468 in shoots) that were differentially expressed under N-free conditions but only 178 genes (63 in roots/115 in shoots) that were differentially expressed under high NH_4^+ conditions within a short period of 4 h after each treatment. It has also been reported that the expression of 166, 553, and 722 genes was changed in shoots exposed to low N conditions (×1/4, ×1/16, and ×1/64) for 5 days and that 10, 5, and 58 genes were differentially expressed under high-N conditions (×4, ×16, and ×64) (**Fig. 1**). These results indicated that marked and rapid changes in gene expression are necessary for adaptation to N deficiency within a short period, but not for adaptation to High N. On the other hand, with regard to longer periods of treatment, Xin *et al.* (2019a) recently demonstrated that the expression of 696 and 808 genes changed in roots after 30 days of exposure to low and high N conditions, respectively.

A total of 3518 differential expressed genes (DEGs) were identified in both shoots and roots of rice seedlings under N-deficient conditions, but only 462 genes (13.1% of the total) showed overlapped expression in both sample types (Cai *et al.* 2012). In addition, 1,158 genes were differentially expressed in leaf sheaths and 492 genes in roots under N starvation, and among them, only 36 genes were shared between the samples (Yang *et al.* 2015b). These results suggested that genes identified as DEGs in each organ contributed specific functions to facilitate distinct response strategies for adaptation to N starvation. In shoots, many genes involved in protein biosynthesis, carbohydrate metabolism, amino acid metabolism and photosynthesis were down-regulated, whereas key genes associated with amino acid degradation were up-regulated in N deficiency (Takehisa *et al.* 2015, Xin *et al.* 2019b). Carbon metabolism such as the tricarboxylic acid (TCA) cycle regulates the nitrogen assimilation pathway by providing α-ketoglutarate for GS/GOGAT cycle and the expression of key genes related to TCA cycle were promoted under low N condition, thereby enhancing the nitrogen assimilation (Xin *et al.* 2019b). Xin *et al.* (2019a) demonstrated that in rice roots the expression of many key genes and metabolite in phenylpropanoid biosynthesis pathway were changed depending on N concentration and proposed that the differences in phenylpropanoid metabolism are the main factors causing optimization of root architecture in response to N availability. In *Arabidopsis*, it has been reported that the activities of N remobilization enzymes are promoted in shoots, allowing root growth using transported amino acids (Krapp *et al.* 2011). The results obtained by

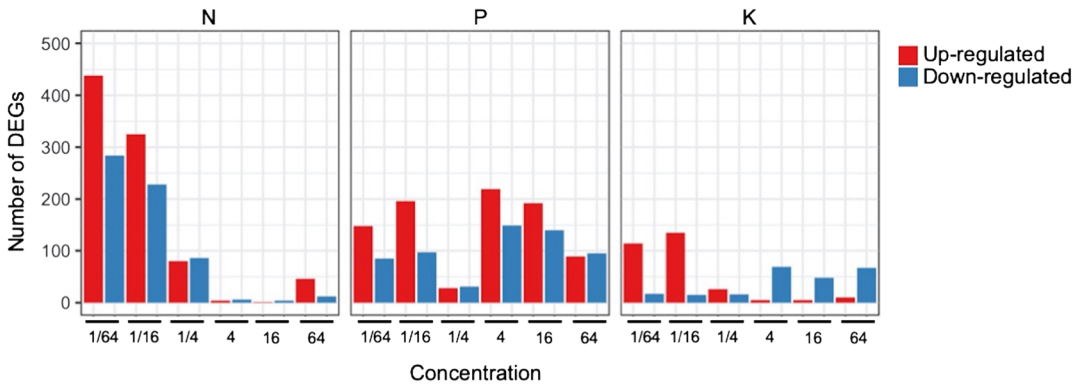

Fig. 1. Number of differentially expressed genes (DEGs) in shoots at 5 days after treatment with varying concentrations (×1/64, ×1/16, ×1/4, ×4, ×16, ×64 of control condition) of N, P and K, respectively (modified from Takehisa 2019). Seven-day old seedlings grown under a normal nutrient condition were subjected to N, P, and K deficiency and excess treatments (Takehisa *et al.* 2015, Takehisa and Sato 2019). One-way ANOVA and fold change (FC) analysis in each nutrient experiment identified 979 probes (805 genes) for N (FC > 5), 798 probes (691 genes) for P (FC > 3), and 328 probes (285 genes) for K (FC > 3), respectively (Takehisa and Sato 2019).

the studies with transcriptome and metabolome analyses account for the observed increase in the root/shoot ratio under N deficiency conditions.

Response to phosphorus

P is a constituent of molecules such as ATP, nucleic acids, and membrane lipids, and is associated with fundamental processes such as signal transduction, photosynthesis and respiration. P deficiency induces various morphological and physiological responses in plants, such as growth retardation, modification of the RSA, secretion of organic acids and phosphatases from roots into the soil to increase Pi uptake, and replacement of phospholipid with non-phosphorous lipids for Pi recycling (Chiou and Lin 2011, Härtel *et al.* 2000, Plaxton and Tran 2011, Poirier and Bucher 2002, Rouached *et al.* 2010). In rice, it has been reported that under P deficient condition plant height and shoot biomass are decreased whereas lateral root elongation of seminal roots is promoted in order to increase the surface area in contact with the soil for efficient Pi acquisition (Hu and Chu 2011, Li *et al.* 2009). In addition, tiller bud outgrowth is inhibited under conditions of P deficiency via the strigolactone-mediated pathway (Umehara *et al.* 2010). On the other hands, it has been demonstrated that excess P supply reduces growth of primary and lateral roots in *Arabidopsis* (Shukla *et al.* 2017).

Signaling pathways under conditions of P deficiency

The molecular mechanisms underlying sensing, signaling and adaptation to P deficiency have been well studied. PHOSPHATE STARVATION RESPONSE1 (PHR1) in *Arabidopsis* is a MYB transcription factor playing key roles in the regulation of P-starvation signaling and P homeostasis by binding to a cis-element via the PHR1 binding site (P1BS) (Bari *et al.* 2006, Bustos *et al.* 2010, Rubio *et al.* 2001). PHR1 regulates downstream genes and non-coding RNAs including SPX (SYG/PHO81/XPR1) domain genes (*SPXs*), phosphate transporters (*PTs*/*PHT*s), purple acid phosphatases (*PAP*s), *INDUCED BY PHOSPHATE STARVATION1* (*IPS1*) (Bari *et al.* 2006, Bustos *et al.* 2010, Nilsson *et al.* 2007, Rubio *et al.* 2001), and miRNAs (Kuo and Chiou 2011). *miRNA399*, in particular, is induced by P starvation via the PHR1-mediated signaling pathway and suppresses its target *PHOSPHATE2* (*PHO2*), which encodes a ubiquitin-conjugating enzyme (Aung *et al.* 2006, Bari *et al.* 2006, Chiou *et al.* 2006, Fujii *et al.* 2005, Lin *et al.* 2008). PHO2 degrades PHO1, a protein involved in the xylem loading of P, and promote the degradation of PHT1 proteins (Huang *et al.* 2013, Liu *et al.* 2012). In rice, a number of key genes such as *OsPHR1* and *OsPHR2*, homologs of *PHR1* (Zhou *et al.* 2008), *OsPHO2/LEAF TIP NECROSIS1* (*LTN1*) (Cao *et al.* 2014, Hu *et al.* 2011), *OsIPS1/2* (Hou *et al.* 2005), *SPX1-3* and *SPX5-6* (Liu *et al.* 2010, Wang *et al.* 2009a, 2009b, 2012), *OsPTs* (Liu *et al.* 2011, Paszkowski *et al.* 2002) and *OsPAPs* (Zhang *et al.* 2011) have been identified and characterized.

Expression signature of the genes responsive to P conditions

As is the case for N, a number of studies have used transcriptome analysis to clarify plant responses and adaptation to conditions where P is absent and/or low (**Table 1**). After 6 h of exposure to P deficiency, several genes related to iron homeostasis such as iron transporter and ferritins were shown to be upregulated in both roots and shoots, and expression of high-affinity Pi transporter genes (*OsPT1* and *OsPT4*) was induced at 24 h (Secco *et al.* 2013, Takehisa *et al.* 2013). Then, at 3 days, the expression of non-coding RNA *IPS1* and high-affinity Pi transporter genes (*OsPT3* and *OsPT6*) was increased. Under long-term P deficiency (for 7 days or more), a large number of genes were differentially expressed, and well-known genes and non-coding RNAs such as *OsPT3*, *OsPT10*,

MONOGALACTOSYLDIACYLGLYCEROL SYNTHASE 2 (*MGD2*), and *IPS1* were markedly upregulated (more than 150-fold) at 21 days (Secco *et al.* 2013). Functional categories overrepresented among the genes upregulated under P deficiency were lipid metabolism, phenylpropanoid metabolism, cytochrome P450 and transport functions in *Arabidopsis* and rice (Misson *et al.* 2005, Morcuende *et al.* 2007, Secco *et al.* 2013). Furthermore, Secco *et al.* (2013) analyzed the transcriptome of samples after Pi resupply to plants after P deficiency for 21 days and identified some transcription factor genes including *WRKY*s and *MYB*s that had been specifically expressed as early as 1 h after Pi resupply. Comparison among rice cultivars with different responses to P deficiency revealed that a number of genes involved in phospholipid remobilization and modulation of the RSA (Mehra *et al.* 2016) and several genes associated with the TCA cycle (Li *et al.* 2010) were highly expressed in the tolerant cultivars.

Response to potassium

K is present in high amounts in plant cells (2–10% of plant dry weight) and is absolutely required for plant growth (Leigh and Wyn Jones 1984). It plays crucial roles in many physiological processes in living plant cells, including osmotic adjustment, enzyme activation, and regulation of cellular pH and cation-anion balance. K deficiency affects shoot and root development and leads to reduced leaf area, interveinal chlorosis, curling of leaf tips, and reduced root growth (Cakmak *et al.* 1994, Hu *et al.* 2016, Jung *et al.* 2009, Zhao *et al.* 2016). However, unlike N or P deficiency, K deficiency does not lead to major alterations in gene expression levels in both *Arabidopsis* and rice (Armengaud *et al.* 2004, Gierth *et al.* 2005, Ma *et al.* 2012, Takehisa *et al.* 2013). Recently, Nishida *et al.* (2017) performed genome-wide analysis of exon combination patterns in response to several nutrient deficiency conditions in *Arabidopsis* and revealed that a number of genes including *MYB* transcription factor genes showed differential alternative splicing only in low K condition. Therefore, these results suggested that most of the initial response to K deficiency might be post-transcriptional and/or post-translational. It has been reported that only a few genes are regulated by short-term K deficiency, including the genes encoding high-affinity potassium transporters such as HKT and HAK, calcium sensor protein, peroxidase involved in scavenging of reactive oxygen species (ROS), protein kinase, and phosphatase in rice (Ma *et al.* 2012, Takehisa *et al.* 2013); the transcript levels of *OsHAK1*, *OsHAK5*, *OsHAK7* and *OsHAK16* are significantly increased in roots under K deficiency (Bañuelos *et al.* 2002, Okada *et al.* 2008, Yang *et al.* 2014). In *Arabidopsis*, signal transduction induced via the CBL (calcineurin B-like protein)-CIPK (CBL-interacting protein kinase) complex has been shown to mediate the phosphorylation of high-affinity K channel AKT1, thus promoting the absorption of K (Li *et al.* 2006, Xu *et al.* 2006). In rice, OsAKT1, has also been shown to play a critical role in K uptake (Li *et al.* 2014). Also, a member of the type III peroxidase family, RCI3, is involved in the production of ROS, which can directly activate a high-affinity K transporter gene, *AtHAK5*, through RAP2.11, a AP2-EREBP transcription factor (Kim *et al.* 2010, 2012).

Common and differing features of responses to varied N, P, and K conditions

In comparison with P and K, N deficiency dramatically and rapidly alters gene expression. In fact, one study has shown that 982 and 592 genes were differentially expressed in roots and shoots, respectively, at 1 h after exposure to N deficiency (Cai *et al.* 2012). On the other hand, the expression of only several dozen or fewer genes was found to change at 24 h after exposure to P deficiency, although there were a number of DEGs at 3 days or more (179 in shoots and 91 in root at 3 days, and 953 and 689, respectively, at 7 days) (Secco *et al.* 2013). Transcriptome analysis using the same experimental platform showed that while 1245 and 1946 genes were differentially expressed in roots at 6 h and 24 h after exposure to N deficiency, respectively, only one and 382 DEGs were identified at 6 h and 24 h after exposure to P deficiency, respectively (Takehisa *et al.* 2013). As is the case for P, only a few genes were differentially expressed at 6 h after exposure to K deficiency. In addition, in rice shoots, differences in expression profiles were evident in response to excess and deficiency of N, P, and K at 5 days after the treatment (**Fig. 1**). The expression of a number of genes was up- and down-regulated under N deficiency, but far fewer genes showed expression changes under N excess condition. The number of DEGs extracted under P deficiency was similar to that under P excess condition. Interestingly, DEGs tended to be up- and down-regulated under conditions of K deficiency and excess, respectively.

Although significant differences were observed in the response to each nutrient condition, one notable feature was that genes related to the regulation of ROS levels were commonly among those that were up-regulated under not only K deficiency but also N and P deficiency (Takehisa *et al.* 2013). *OsGLP1* encoding a germin-like protein was strongly up-regulated under each type of nutrient deficiency, and is reportedly associated with biotic and abiotic stress tolerance via hyper-accumulation of hydrogen peroxide (Banerjee *et al.* 2010a, Banerjee and Maiti 2010b). As is the case for K, class-III peroxidase genes and *RAP2.11* were also upregulated under conditions of N and P deficiency. Therefore, the ROS signaling pathway may play an important role in adaptation to macronutrient deficiencies.

Root system architecture

Roots are essential for plant growth and development,

anchoring plants to growth substrates, promoting the uptake of water and nutrients from the soil, and responding to biotic and abiotic stresses. Root architectural and physiological characteristics are closely related to nutrient uptake and allocation, growth and yield in crop plants. Modifications to the RSA under nutrient deficiency are complex, and dependent on plant species and experimental conditions (i.e. nutrient concentration). In rice, N and P deficiency leads to elongation of the primary (seminal) root (Niu *et al.* 2013, Sun *et al.* 2014, 2016, Zhang *et al.* 2012) and changes in lateral root length and density (Mehra *et al.* 2016, Sun *et al.* 2014). Nitric oxide (NO) is a signaling molecule involved in many physiological processes during root development and nutrient assimilation (Bai *et al.* 2014, Correa-Aragunde *et al.* 2004, Fernández-Marcos *et al.* 2011, Frungillo *et al.* 2014, Jin *et al.* 2009, Lombardo *et al.* 2006, Manoli *et al.* 2014, Pagnussat *et al.* 2002, 2003). NO induced by N and P deficiencies is positively correlated with elongation of the seminal roots in rice, via a pathway mediated by a plant hormone, strigolactone (Sun *et al.* 2014, 2016).

The rice root system is composed of the seminal root, crown root, lateral root and root hair, all derived from different cells. Thus, to fully clarify the mechanisms responsible for morphological changes in roots, information on gene expression in each cell type is required. Root cell-type transcriptome profiling has been performed for *Arabidopsis* (Birnbaum *et al.* 2003, Brady *et al.* 2007, Dinneny *et al.* 2008, Gifford *et al.* 2008, Nawy *et al.* 2005), rice (Takehisa *et al.* 2012) and maize (Dembinsky *et al.* 2007, Yu *et al.* 2015, 2016, Woll *et al.* 2005). In rice, tissue- and cell-type transcriptome analysis has been conducted using a combination of laser microdissection and microarray analysis (Takehisa *et al.* 2012). In that study, crown roots were divided into 8 parts with different developmental stages along the longitudinal axis and 3 radial tissue types, i.e., epidermis, exodermis and sclerenchyma; cortex; and endodermis, pericycle and stele. Expression profiling of the samples defined major sites for uptake and transport of nutrients as well as the radial transport system from the rhizosphere to the xylem vessels specific for each nutrient. In addition, 2 gene sets were identified; one contains 71 genes such as *CROWN ROOTLESS 1/ADVENTITIOUS ROOTLESS 1* (*CRL1/ARL1*) (Inukai *et al.* 2005, Liu *et al.* 2005) and a homolog of *Arabidopsis PUCHI* (Hirota *et al.* 2007), which have function in lateral root formation, and the other set contains 78 genes, many of which were associated with cell division and root elongation (Takehisa *et al.* 2012). Expression profiling of these gene sets with a dataset, which consists of various organs/tissue sample data (Sato *et al.* 2011a, 2011b), revealed that the former was expressed specifically in roots whereas the latter was expressed in immature organs at the reproductive/ripening stages (**Fig. 2**), thereby further supporting the possibility that the former genes are specifically associated with lateral root formation whereas the latter function in cell division and elongation in whole tissues. Moreover, it was reported that several of the above 71 genes are differentially regulated in the *Osiaa13* mutant compared with the wild type, indicating that these may function in lateral root initiation via an OsIAA13-mediated auxin signaling pathway (Kitomi *et al.* 2012). Furthermore, these gene sets were used for

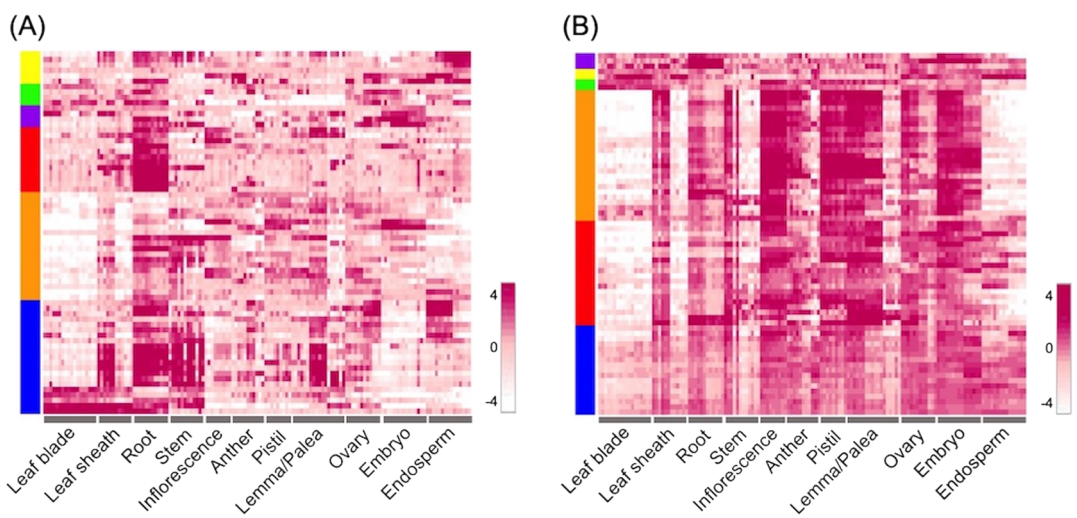

Fig. 2. Expression profile of 71 genes functioning specifically in lateral root formation (A) and 78 genes associated with root cell division and elongation (B) based on transcriptome data for various organs and tissues at different developmental stages. The 71 and 78 genes were identified by Takehisa *et al.* (2012). The data for various organs and tissues consist of 143 microarray data derived from the leaf blade (6 samples), leaf sheath (4) root (4), stem (3), panicle (3), anther (3), pistil (3), lemma and palea (6), ovary (4), embryo (5), and endosperm (5) (Sato *et al.* 2011a). The vegetative and reproductive organ samples were derived mainly from samples at the mature and immature stages of development, respectively. Expression data were applied to 75th percentile normalization, and log2 transformation. The relative expression value (log2) was obtained by subtracting the median expression value within the dataset for each probe. The 71 and 78 genes were divided into 6 clusters based on similarity of expression pattern, respectively, and each cluster was colored in different colors.

comparison between two cultivars with different responses to P deficiency (Mehra *et al.* 2016). Thus, utilization of transcriptome data for different attribute types can provide more insight into genes of interest. Further details are described below.

Meta- and co-expression analyses across distinct datasets

Expression profiling of DEGs in other datasets is useful for their classification based on transcriptional level and depth understanding of their functions. In addition, coexpression analysis across multiple datasets is a powerful approach for predicting the function of unknown genes and for identifying key genes and/or modules related to specific biological events of interest (Eisen *et al.* 1998). These strategies have been proved to reveal novel factors regulating specific metabolic pathways in *Arabidopsis* (Amrine *et al.* 2015, Aoki *et al.* 2007, Hirai *et al.* 2007, Obayashi and Kinoshita 2010, Shaik and Ramakrishna 2013, Sharma *et al.* 2018). In rice, these types of approach have also been used for identification and characterization of genes and/or gene networks (Buti *et al.* 2019, Cohen and Leach 2019, de Abreu Neto and Feri 2016, Narsai *et al.* 2013, Takehisa *et al.* 2013, 2015, Zhu *et al.* 2019). Expression profiling of genes responsive to macronutrient stress (N, P and K deficiency) in the root in response to phytohormones such as abscisic acid (ABA), gibberellic acid (GA), auxin (IAA), brassinosteroid (BR), cytokinin (CK) and jasmonate (JA) has indicated that responses to K deficiency may be related to the signal transduction pathway mediated by JA (Takehisa *et al.* 2013). DEGs identified in shoots under macronutrient deficiency were applied to co-expression analysis by adding datasets for various organs and tissues at different stages of development (Takehisa *et al.* 2015). This identified several modules, which mostly comprised genes down-regulated under N deficiency, with distinct functions such as development of immature organs, protein biosynthesis and photosynthesis in chloroplast of green tissues, as well as fundamental cellular processes in all organs and tissues. One of these modules contained a number of protein kinase genes and nutrient transporter genes encoding ammonium transporter (OsAMT1;2 and OsAMT3;3), phosphate transporter (OsPT8), and potassium transporter (OsHAK27). In *Arabidopsis*, phosphorylation-dependent regulation has been reported for transporters/channels related to the transport of nitrate (NRT1;1/CHL1), potassium (AKT1) and ammonium (AMT1;1) under conditions of nutrient deficiency (Lanquar *et al.* 2009, Lee *et al.* 2007, Liu and Tsay 2003, Loqué *et al.* 2007). These results imply that the co-expressed genes may play a role in the nutrient usage mechanism under conditions of nutrient deprivation.

A large number of transcriptome data covering various organs and tissues, and experimental conditions such as biotic and abiotic stress, are now available in the public domain including NCBI-GEO (Barrett *et al.* 2013) and ArrayExpress (Kolesnikov *et al.* 2015). Moreover, several databases for gene expression in rice, such as RiceXPro (Sato *et al.* 2011a, 2013a), OryzaExpress (Hamada *et al.* 2011), ROAD (Cao *et al.* 2012), Expression Atlas (Petryszak *et al.* 2016), TENOR (Kawahara *et al.* 2016), and RED (Xia *et al.* 2017) have been developed. In addition, rice gene coexpression data are available from ATTED-II (Obayashi *et al.* 2011), OryzaExpress (Hamada *et al.* 2011), RiceFREND (Sato *et al.* 2013b), RECoN (Krishnan *et al.* 2017), and RiceAntherNet (Lin *et al.* 2017). Therefore, further analysis of nutrient-responsive genes using this type of transcriptome resource will be useful for gaining a deeper understanding of when and how plants respond and adapt to variable nutritional conditions.

Understanding nutrient status dynamics in the field

As described above, there is now a large volume of transcriptome data relating to nutrient deficiency or supply, making it easier to study the mechanisms of adaptive response and tolerance and identify the genes associated with these events (**Table 1**). However, most of the studies were based on transcriptome analysis using samples derived from seedling plants under laboratory conditions over a relatively short period of time. In contrast, under field conditions, crop plants respond to multiple factors simultaneously over a long period throughout their vegetative, reproductive, and ripening stages. In addition, it has been shown that the adaptive responses of crop plants to nutrient conditions vary among different genetic backgrounds and/or growth stages. Therefore, it is important to understand when nutrient-responsive genes identified under laboratory conditions are expressed and how their expression is associated with biological events, such as tillering, flowering, and ripening for rice, which occur during the process of growth. There is a large volume of transcriptome data for rice derived from leaf samples during the entire period of growth under field conditions (Nagano *et al.* 2012, Sato *et al.* 2011b, 2013a). To identify the network of core nutrient-response genes under both laboratory and field conditions, co-expression analysis of 1452 macronutrient-responsive genes identified in the laboratory was performed using time-course transcriptome data for rice obtained in the field (Takehisa and Sato 2019). This analysis successfully identified 3 biomarker gene sets for monitoring the N and P status of rice plants under field conditions, including about 10 genes in each set, and profiling of the biomarker genes made it possible to visualize growth-stage and soil condition-dependent changes in nutrient status (Takehisa and Sato 2019). Notably, the biomarker gene set for P contained P deficiency responsive genes such as *OsSPX1* and *MGD2*, which is a close homologue of Arabidopsis *MGD2* and *MGD3* associated with replacement of phospholipid with non-phosphorous lipids for Pi recycling (Kobayashi *et al.* 2009), were up-regulated

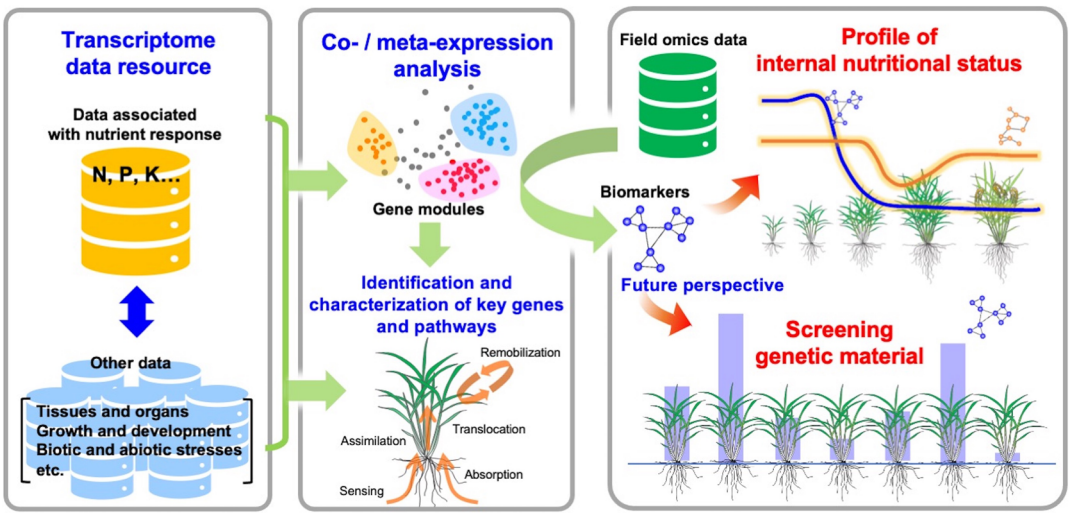

Fig. 3. An overview of the transcriptome-based approach for understanding the molecular mechanisms of response and adaptation to the nutritional environment and improvement of crop production.

during the tillering stage in rice grown under soil conditions with a high phosphate retention capacity, indicating that rice plants express a system for acquisition and recycling to compensate the P required for tiller development under such field conditions (Takehisa and Sato 2019).

Conclusion and future perspectives

Transcriptome profiling has contributed to the identification of key genes/pathways associated with the response and adaptation of plants to varied nutrient conditions and alterations of root system architecture important for uptake of nutrients from the rhizosphere (Fig. 3). Furthermore, meta- and co-expression analyses using different data makes it possible to highlight nutrient-responsive genes and identify modules that are related to a common biological process, and data resource available for such the analysis has been developed. As crop plants grow under field conditions, phenomena observed during the growth process are complex. To improve the nutrient use efficiency of crop plants and enhance their tolerance to nutrient deficiency, it would be important to not only isolate genetic materials with better performance in such traits but also understand when and how plants respond and adapt to nutritional conditions. Omics studies focusing on the transcriptome, proteome, and metabolome would be a powerful approach for profiling of the molecular dynamics that reflect internal status, thereby enabling the development of suitable biomarkers for evaluation of nutrient conditions of plants under field conditions. Indeed, profiling of N and P biomarkers developed on the basis of transcriptome data has revealed soil- and growth-stage-dependent changes in nutrient status (Takehisa and Sato 2019). The information of internal status obtained by biomarker profiling might be useful for cultivation management. More recently, it has been demonstrated that transcriptome data would be useful for not only genomic prediction but also providing a link between traits and variation (Azodi *et al.* 2020). Therefore, transcriptome-based approach would also have a potential for screening genetic materials of interest and thus has considerable applicability to the breeding of crop plants with various traits including nutritional characteristics that can complement a genetics-based approach.

Author Contribution Statement

HT constructed figures and table; HT and YS wrote the manuscript.

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Literature Cited

Amrine, K.C.H., B. Blanco-Ulate and D. Cantu (2015) Discovery of core biotic stress responsive genes in Arabidopsis by weighted gene co-expression network analysis. PLoS ONE 10: e0118731.

Aoki, K., Y. Ogata and D. Shibata (2007) Approaches for extracting practical information from gene co-expression networks in plant biology. Plant Cell Physiol. 48: 381–390.

Armengaud, P., R. Breitling and A. Amtmann (2004) The potassium-dependent transcriptome of Arabidopsis reveals a prominent role of jasmonic acid in nutrient signaling. Plant Physiol. 136: 2556–2576.

Aung, K., S.I. Lin, C.C. Wu, Y.T. Huang, C.L. Su and T.J. Chiou (2006) *pho2*, a phosphate overaccumulator, is caused by a nonsense mutation in a microRNA399 target gene. Plant Physiol. 141: 1000–1011.

Azodi, C.B., J. Pardo, R. VanBuren, G. de Los Campos and S.H. Shiu (2020) Transcriptome-based prediction of complex traits in maize. Plant Cell 32: 139–151.

Bai, S., T. Yao, M. Li, X. Guo, Y. Zhang, S. Zhu and Y. He (2014) PIF3 is involved in the primary root growth inhibition of *Arabidopsis* induced by nitric oxide in the light. Mol. Plant 7: 616–625.

Banerjee, J., N. Das, P. Dey and M.K. Maiti (2010a) Transgenically expressed rice germin-like protein1 in tobacco causes hyper-accumulation of H_2O_2 and reinforcement of the cell wall components. Biochem. Biophys. Res. Commun. 402: 637–643.

Banerjee, J. and M.K. Maiti (2010b) Functional role of rice germin-like protein1 in regulation of plant height and disease resistance. Biochem. Biophys. Res. Commun. 394: 178–183.

Bañuelos, M.A., B. Garciadeblas, B. Cubero and A. Rodríguez-Navarro (2002) Inventory and functional characterization of the HAK potassium transporters of rice. Plant Physiol. 130: 784–795.

Bari, R., B. Datt Pant, M. Stitt and W.R. Scheible (2006) PHO2, microRNA399, and PHR1 define a phosphate-signaling pathway in plants. Plant Physiol. 141: 988–999.

Barrett, T., S.E. Wilhite, P. Ledoux, C. Evangelista, I.F. Kim, M. Tomashevsky, K.A. Marshall, K.H. Phillippy, P.M. Sherman, M. Holko *et al.* (2013) NCBI GEO: archive for functional genomics data sets—update. Nucleic Acids Res. 41: D991–D995.

Birnbaum, K., D.E. Shasha, J.Y. Wang, J.W. Jung, G.M. Lambert, D.W. Galbraith and P.N. Benfey (2003) A gene expression map of the *Arabidopsis* root. Science 302: 1956–1960.

Brady, S.M., D.A. Orlando, J.Y. Lee, J.Y. Wang, J. Koch, J.R. Dinneny, D. Mace, U. Ohler and P.N. Benfey (2007) A high-resolution root spatiotemporal map reveals dominant expression patterns. Science 318: 801–806.

Bustos, R., G. Castrillo, F. Linhares, M.I. Puga, V. Rubio, J. Pérez-Pérez, R. Solano, A. Leyva and J. Paz-Ares (2010) A central regulatory system largely controls transcriptional activation and repression responses to phosphate starvation in Arabidopsis. PLoS Genet. 6: e1001102.

Buti, M., E. Baldoni, E. Formentin, J. Milc, G. Frugis, F.L. Schiavo, A. Genga and E. Francia (2019) A meta-analysis of comparative transcriptomic data reveals a set of key genes involved in the tolerance to abiotic stresses in rice. Int. J. Mol. Sci. 20: 5662.

Cai, H., Y. Lu, W. Xie, T. Zhu and X. Lian (2012) Transcriptome response to nitrogen starvation in rice. J. Biosci. 37: 731–747.

Cakmak, I., C. Hengeler and H. Marschner (1994) Partitioning of shoot and root dry matter and carbohydrates in bean plants suffering from phosphorus, potassium and magnesium deficiency. J. Exp. Bot. 45: 1245–1250.

Canales, J., T.C. Moyano, E. Villarroel and R.A. Gutiérrez (2014) Systems analysis of transcriptome data provides new hypotheses about *Arabidopsis* root response to nitrate treatments. Front. Plant Sci. 5: 22.

Cao, P., K.H. Jung, D. Choi, D. Hwang, J. Zhu and P.C. Ronald (2012) The rice oligonucleotide array database: an atlas of rice gene expression. Rice (N Y) 5: 17.

Cao, Y., Y. Yan, F. Zhang, H.D. Wang, M. Gu, X.N. Wu, S.B. Sun and G.H. Xu (2014) Fine characterization of *OsPHO2* knockout mutants reveals its key role in Pi utilization in rice. J. Plant Physiol. 171: 340–348.

Chandran, A.K., R.A. Priatama, V. Kumar, Y.H. Xuan, B.I. Je, C.M. Kim, K.H. Jung and C.D. Han (2016) Genome-wide transcriptome analysis of expression in rice seedling roots in response to supplemental nitrogen. J. Plant Physiol. 200: 62–75.

Chiou, T.J., K. Aung, S.I. Lin, C.C. Wu, S.F. Chiang and C.L. Su (2006) Regulation of phosphate homeostasis by microRNA in *Arabidopsis*. Plant Cell 18: 412–421.

Chiou, T.J. and S.I. Lin (2011) Signaling network in sensing phosphate availability in plants. Annu. Rev. Plant Biol. 62: 185–206.

Cohen, S.P. and J.E. Leach (2019) Abiotic and biotic stresses induce a core transcriptome response in rice. Sci. Rep. 9: 6273.

Correa-Aragunde, N., M. Graziano and L. Lamattina (2004) Nitric oxide plays a central role in determining lateral root development in tomato. Planta 218: 900–905.

Dai, X., Y. Wang, A. Yang and W.H. Zhang (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 Abreu Neto, J.B. and M. Frei (2016) Microarray meta-analysis focused on the response of genes involved in redox homeostasis to diverse abiotic stresses in rice. Front. Plant Sci. 6: 1260.

Dembinsky, D., K. Woll, M. Saleem, Y. Liu, Y. Fu, L.A. Borsuk, T. Lamkemeyer, C. Fladerer, J. Madlung, B. Barbazuk *et al.* (2007) Transcriptomic and proteomic analyses of pericycle cells of the maize primary root. Plant Physiol. 145: 575–588.

Deng, Q.W., X.D. Luo, Y.L. Chen, Y. Zhou, F.T. Zhang, B.L. Hu and J.K. Xie (2018) Transcriptome analysis of phosphorus stress responsiveness in the seedlings of Dongxiang wild rice (*Oryza rufipogon* Griff.). Biol. Res. 51: 7.

Dinneny, J.R., T.A. Long, J.Y. Wang, J.W. Jung, D. Mace, S. Pointer, C. Barron, S.M. Brady, J. Schiefelbein and P.N. Benfey (2008) Cell identity mediates the response of *Arabidopsis* roots to abiotic stress. Science 320: 942–945.

Eisen, M.B., P.T. Spellman, P.O. Brown and D. Botstein (1998) Cluster analysis and display of genome-wide expression patterns. Proc. Natl. Acad. Sci. USA 95: 14863–14868.

Fan, X., H. Feng, Y. Tan, Y. Xu, Q. Miao and G. Xu (2015) A putative 6-transmembrane nitrate transporter OsNRT1.1b plays a key role in rice under low nitrogen. J. Integr. Plant Biol. 58: 590–599.

Feng, H., M. Yan, X. Fan, B. Li, Q. Shen, A.J. Miller and G. Xu (2011) Spatial expression and regulation of rice high-affinity nitrate transporters by nitrogen and carbon status. J. Exp. Bot. 62: 2319–2332.

Fernández-Marcos, M., L. Sanz, D.R. Lewis, G.K. Muday and O. Lorenzo (2011) Nitric oxide causes root apical meristem defects and growth inhibition while reducing PIN-FORMED 1 (PIN1)-dependent acropetal auxin transport. Proc. Natl. Acad. Sci. USA 108: 18506–18511.

Frungillo, L., M.J. Skelly, G.J. Loake, S.H. Spoel and I. Salgado (2014) *S*-nitrosothiols regulate nitric oxide production and storage in plants through the nitrogen assimilation pathway. Nat. Commun. 5: 5401.

Fujii, H., T.J. Chiou, S.I. Lin, K. Aung and J.K. Zhu (2005) A miRNA involved in phosphate-starvation response in *Arabidopsis*. Curr. Biol. 15: 2038–2043.

Gelli, M., Y. Duo, A.R. Konda, C. Zhang, D. Holding and I. Dweikat (2014) Identification of differentially expressed genes between sorghum genotypes with contrasting nitrogen stress tolerance by genome-wide transcriptional profiling. BMC Genomics 15: 179.

Giehl, R.F.H. and N.V. Wirén (2014) Root nutrient foraging. Plant Physiol. 166: 509–517.

Gierth, M., P. Mäser and J.I. Schroeder (2005) The potassium transporter *AtHAK5* functions in K^+ deprivation-induced high-affinity K^+ uptake and *AKT1* K^+ channel contribution to K^+ uptake kinetics in Arabidopsis roots. Plant Physiol. 137: 1105–1114.

Gifford, M.L., A. Dean, R.A. Gutiérrez, G.M. Coruzzi and K.D. Birnbaum (2008) Cell-specific nitrogen responses mediate developmental plasticity. Proc. Natl. Acad. Sci. USA 105: 803–808.

Guiboileau, A., K. Yoshimoto, F. Soulay, M.P. Bataillé, J.C. Avice and C. Masclaux-Daubresse (2012) Autophagy machinery controls nitrogen remobilization at the whole-plant level under both limiting and ample nitrate conditions in *Arabidopsis*. New Phytol. 194:

732–740.
Hamada, K., K. Hongo, K. Suwabe, A. Shimizu, T. Nagayama, R. Abe, S. Kikuchi, N. Yamamoto, T. Fujii, K. Yokoyama *et al.* (2011) OryzaExpress: an integrated database of gene expression networks and omics annotations in rice. Plant Cell Physiol. 52: 220–229.
Hammond, J.P., M.J. Bennett, H.C. Bowen, M.R. Broadley, D.C. Eastwood, S.T. May, C. Rahn, R. Swarup, K.E. Woolaway and P.J. White (2003) Changes in gene expression in Arabidopsis shoots during phosphate starvation and the potential for developing smart plants. Plant Physiol. 132: 578–596.
Hao, Q.N., X.A. Zhou, A.H. Sha, C. Wang, R. Zhou and S.L. Chen (2011) Identification of genes associated with nitrogen-use efficiency by genome-wide transcriptional analysis of two soybean genotypes. BMC Genomics 12: 525.
Härtel, H., P. Dörmann and C. Benning (2000) DGD1-independent biosynthesis of extraplastidic galactolipids after phosphate deprivation in Arabidopsis. Proc. Natl. Acad. Sci. USA 97: 10649–10654.
Hirai, M.Y., K. Sugiyama, Y. Sawada, T. Tohge, T. Obayashi, A. Suzuki, R. Araki, N. Sakurai, H. Suzuki, K. Aoki *et al.* (2007) Omics-based identification of *Arabidopsis* Myb transcription factors regulating aliphatic glucosinolate biosynthesis. Proc. Natl. Acad. Sci. USA 104: 6478–6483.
Hirota, A., T. Kato, H. Fukaki, M. Aida and M. Tasaka (2007) The auxin-regulated AP2/EREBP gene *PUCHI* is required for morphogenesis in the early lateral root primordium of *Arabidopsis*. Plant Cell 19: 2156–2168.
Hou, X.L., P. Wu, F.C. Jiao, Q.J. Jia, H.M. Chen, J. Yu, X.W. Song and K.K. Yi (2005) Regulation of the expression of *OsIPS1* and *OsIPS2* in rice via systemic and local Pi signalling and hormones. Plant Cell Environ. 28: 353–364.
Hsieh, P.H., C.C. Kan, H.Y. Wu, H.C. Yang and M.H. Hsieh (2018) Early molecular events associated with nitrogen deficiency in rice seedling roots. Sci. Rep. 8: 12207.
Hu, B. and C. Chu (2011) Phosphate starvation signaling in rice. Plant Signal. Behav. 6: 927–929.
Hu, B., C. Zhu, F. Li, J. Tang, Y. Wang, A. Lin, L. Liu, R. Che and C. Chu (2011) *LEAF TIP NECROSIS1* plays a pivotal role in the regulation of multiple phosphate starvation responses in rice. Plant Physiol. 156: 1101–1115.
Hu, B., W. Wang, S.J. Ou, J.Y. Tang, H. Li, R.H. Che, Z.H. Zhang, X.Y. Chai, H.R. Wang, Y.Q. Wang *et al.* (2015) Variation in *NRT1.1B* contributes to nitrate-use divergence between rice subspecies. Nat. Genet. 47: 834–838.
Hu, W., X.B. Lv, J.S. Yang, B.L. Chen, W.Q. Zhao, Y.L. Meng, Y.H. Wang, Z.G. Zhou and D.M. Oosterhuis (2016) Effects of potassium deficiency on antioxidant metabolism related to leaf senescence in cotton (*Gossypium hirsutum* L.). Field Crops Res. 191: 139–149.
Huang, T.K., C.L. Han, S.I. Lin, Y.J. Chen, Y.C. Tsai, Y.R. Chen, J.W. Chen, W.Y. Lin, P.M. Chen, T.Y. Liu *et al.* (2013) Identification of downstream components of ubiquitin-conjugating enzyme PHOSPHATE2 by quantitative membrane proteomics in *Arabidopsis* roots. Plant Cell 25: 4044–4060.
Inukai, Y., T. Sakamoto, M. Ueguchi-Tanaka, Y. Shibata, K. Gomi, I. Umemura, Y. Hasegawa, M. Ashikari, H. Kitano and M. Matsuoka (2005) *Crown rootless1*, which is essential for crown root formation in rice, is a target of an AUXIN RESPONSE FACTOR in auxin signaling. Plant Cell 17: 1387–1396.
Jin, C.W., S.T. Du, Y.S. Zhang, X.Y. Lin and C.X. Tang (2009) Differential regulatory role of nitric oxide in mediating nitrate reductase activity in roots of tomato (*Solanum lycocarpum*). Ann. Bot. 104: 9–17.
Ju, X.T., G.X. Xing, X.P. Chen, S.L. Zhang, L.J. Zhang, X.J. Liu, Z.L. Cui, B. Yin, P. Christie, Z.L. Zhu *et al.* (2009) Reducing environmental risk by improving N management in intensive Chinese agricultural systems. Proc. Natl. Acad. Sci. USA 106: 3041–3046.
Jung, J.Y., R. Shin and D.P. Schachtman (2009) Ethylene mediates response and tolerance to potassium deprivation in *Arabidopsis*. Plant Cell 21: 607–621.
Kawahara, Y., Y. Oono, H. Wakimoto, J. Ogata, H. Kanamori, H. Sasaki, S. Mori, T. Matsumoto and T. Itoh (2016) TENOR: database for comprehensive mRNA-Seq experiments in rice. Plant Cell Physiol. 57: e7.
Kim, M.J., S. Ciani and D.P. Schachtman (2010) A peroxidase contributes to ROS production during Arabidopsis root response to potassium deficiency. Mol. Plant 3: 420–427.
Kim, M.J., D. Ruzicka, R. Shin and D.P. Schachtman (2012) The *Arabidopsis* AP2/ERF transcription factor RAP2.11 modulates plant response to low-potassium conditions. Mol. Plant 5: 1042–1057.
Kitomi, Y., H. Inahashi, H. Takehisa, Y. Sato and Y. Inukai (2012) OsIAA13-mediated auxin signaling is involved in lateral root initiation in rice. Plant Sci. 190: 116–122.
Kobayashi, K., K. Awai, M. Nakamura, A. Nagatani, T. Masuda and H. Ohta (2009) Type-B monogalactosyldiacylglycerol synthases are involved in phosphate starvation-induced lipid remodeling, and are crucial for low phosphate adaptation. Plant J. 57: 322–331.
Kolesnikov, N., E. Hastings, M. Keays, O. Melnichuk, Y.A. Tang, E. Williams, M. Dylag, N. Kurbatova, M. Brandizi, T. Burdett *et al.* (2015) ArrayExpress update—simplifying data submissions. Nucleic Acids Res. 43: D1113–D1116.
Krapp, A., R. Berthomé, M. Orsel, S. Mercey-Boutet, A. Yu, L. Castaings, S. Elftieh, H. Major, J.P. Renou and F. Daniel-Vedele (2011) Arabidopsis roots and shoots show distinct temporal adaptation patterns toward nitrogen starvation. Plant Physiol. 157: 1255–1282.
Krishnan, A., C. Gupta, M.M.R. Ambavaram and A. Pereira (2017) RECoN: rice environment coexpression network for systems level analysis of abiotic-stress response. Front. Plant Sci. 8: 1640.
Kuo, H.F. and T.J. Chiou (2011) The role of microRNAs in phosphorus deficiency signaling. Plant Physiol. 156: 1016–1024.
Lanquar, V., D. Loqué, F. Hörmann, L. Yuan, A. Bohner, W.R. Engelsberger, S. Lalonde, W.X. Schulze, N. von Wirén and W.B. Frommer (2009) Feedback inhibition of ammonium uptake by a phospho-dependent allosteric mechanism in *Arabidopsis*. Plant Cell 21: 3610–3622.
Lee, S.C., W.Z. Lan, B.G. Kim, L. Li, Y.H. Cheong, G.K. Pandey, G. Lu, B.B. Buchanan and S. Luan (2007) A protein phosphorylation/dephosphorylation network regulates a plant potassium channel. Proc. Natl. Acad. Sci. USA 104: 15959–15964.
Leigh, R.A. and R.G. Wyn Jones (1984) A hypothesis relating critical potassium concentrations for growth to the distribution and functions of this ion in the plant cell. New Phytol. 97: 1–13.
Li, J., Y. Xie, A. Dai, L. Liu and Z. Li (2009) Root and shoot traits responses to phosphorus deficiency and QTL analysis at seedling stage using introgression lines of rice. J. Genet. Genomics 36: 173–183.
Li, J., Y. Long, G.N. Qi, J. Li, Z.J. Xu, W.H. Wu and Y. Wang (2014) The Os-AKT1 channel is critical for K^+ uptake in rice roots and is modulated by the rice CBL1-CIPK23 complex. Plant Cell 26: 3387–3402.
Li, L., C. Liu and X. Lian (2010) Gene expression profiles in rice roots under low phosphorus stress. Plant Mol. Biol. 72: 423–432.
Li, L.G., B.G. Kim, Y.H. Cheong, G.K. Pandey and S. Luan (2006) A

Ca^{2+} signaling pathway regulates a K^+ channel for low-K response in *Arabidopsis*. Proc. Natl. Acad. Sci. USA 103: 12625–12630.

Li, Y., J. Ouyang, Y.Y. Wang, R. Hu, K. Xia, J. Duan, Y. Wang, Y.F. Tsay and M. Zhang (2015) Disruption of the rice nitrate transporter OsNPF2.2 hinders root-to-shoot nitrate transport and vascular development. Sci. Rep. 5: 9635.

Lian, X., S. Wang, J. Zhang, Q. Feng, L. Zhang, D. Fan, X. Li, D. Yuan, B. Han and Q. Zhang (2006) Expression profiles of 10,422 genes at early stage of low nitrogen stress in rice assayed using a cDNA microarray. Plant Mol. Biol. 60: 617–631.

Lin, C.M., S. Koh, G. Stacey, S.M. Yu, T.Y. Lin and Y.F. Tsay (2000) Cloning and functional characterization of a constitutively expressed nitrate transporter gene *OsNRT1* from rice. Plant Physiol. 122: 379–388.

Lin, H., J. Yu, S.P. Pearce, D. Zhang and Z.A. Wilson (2017) RiceAntherNet: a gene co-expression network for identifying anther and pollen development genes. Plant J. 92: 1076–1091.

Lin, S.I., S.F. Chiang, W.Y. Lin, J.W. Chen, C.Y. Tseng, P.C. Wu and T.J. Chiou (2008) Regulatory network of microRNA399 and *PHO2* by systemic signaling. Plant Physiol. 147: 732–746.

Liu, F., Z. Wang, H. Ren, C. Shen, Y. Li, H.Q. Ling, C. Wu, X. Lian and P. Wu (2010) OsSPX1 suppresses the function of OsPHR2 in the regulation of expression of *OsPT2* and phosphate homeostasis in shoots of rice. Plant J. 62: 508–517.

Liu, F., X.J. Chang, Y. Ye, W.B. Xie, P. Wu and X.M. Lian (2011) Comprehensive sequence and whole-life-cycle expression profile analysis of the phosphate transporter gene family in rice. Mol. Plant 4: 1105–1122.

Liu, H., S. Wang, X. Yu, J. Yu, X. He, S. Zhang, H. Shou and P. Wu (2005) ARL1, a LOB-domain protein required for adventitious root formation in rice. Plant J. 43: 47–56.

Liu, K.H. and Y.F. Tsay (2003) Switching between the two action modes of the dual-affinity nitrate transporter CHL1 by phosphorylation. EMBO J. 22: 1005–1013.

Liu, T.Y., T.K. Huang, C.Y. Tseng, Y.S. Lai, S.I. Lin, W.Y. Lin, J.W. Chen and T.J. Chiou (2012) PHO2-dependent degradation of PHO1 modulates phosphate homeostasis in *Arabidopsis*. Plant Cell 24: 2168–2183.

Lombardo, M.C., M. Graziano, J.C. Polacco and L. Lamattina (2006) Nitric oxide functions as a positive regulator of root hair development. Plant Signal. Behav. 1: 28–33.

Loqué, D., S. Lalonde, L.L. Looger, N. von Wirén and W.B. Frommer (2007) A cytosolic trans-activation domain essential for ammonium uptake. Nature 446: 195–198.

Luan, S., W. Lan and S.C. Lee (2009) Potassium nutrition, sodium toxicity, and calcium signaling: connections through the CBL-CIPK network. Curr. Opin. Plant Biol. 12: 339–346.

Lynch, J.P. (2011) Root phenes for enhanced soil exploration and phosphorus acquisition: tools for future crops. Plant Physiol. 156: 1041–1049.

Ma, T.L., W.H. Wu and Y. Wang (2012) Transcriptome analysis of rice root responses to potassium deficiency. BMC Plant Biol. 12: 161.

Manoli, A., M. Begheldo, A. Genre, L. Lanfranco, S. Trevisan and S. Quaggiotti (2014) NO homeostasis is a key regulator of early nitrate perception and root elongation in maize. J. Exp. Bot. 65: 185–200.

Mehra, P., B.K. Pandey and J. Giri (2016) Comparative morphophysiological analyses and molecular profiling reveal Pi-efficient strategies of a traditional rice genotype. Front. Plant Sci. 6: 1184.

Misson, J., K.G. Raghothama, A. Jain, J. Jouhet, M.A. Block, R. Bligny, P. Ortet, A. Creff, S. Somerville, N. Rolland *et al.* (2005) A genome-wide transcriptional analysis using *Arabidopsis thaliana* Affymetrix gene chips determined plant responses to phosphate deprivation. Proc. Natl. Acad. Sci. USA 102: 11934–11939.

Morcuende, R., R. Bari, Y. Gibon, W. Zheng, B.D. Pant, O. Bläsing, B. Usadel, T. Czechowski, M.K. Udvardi, M. Stitt *et al.* (2007) Genome-wide reprogramming of metabolism and regulatory networks of *Arabidopsis* in response to phosphorus. Plant Cell Environ. 30: 85–112.

Nagano, A.J., Y. Sato, M. Mihara, B.A. Antonio, R. Motoyama, H. Itoh, Y. Nagamura and T. Izawa (2012) Deciphering and prediction of transcriptome dynamics under fluctuating field conditions. Cell 151: 1358–1369.

Nakatogawa, H., K. Suzuki, Y. Kamada and Y. Ohsumi (2009) Dynamics and diversity in autophagy mechanisms: lessons from yeast. Nat. Rev. Mol. Cell Biol. 10: 458–467.

Narsai, R., C. Wang, J. Chen, J. Wu, H. Shou and J. Whelan (2013) Antagonistic, overlapping and distinct responses to biotic stress in rice (*Oryza sativa*) and interactions with abiotic stress. BMC Genomics 14: 93.

Nawy, T., J.Y. Lee, J. Colinas, J.Y. Wang, S.C. Thongrod, J.E. Malamy, K. Birnbaum and P.N. Benfey (2005) Transcriptional profile of the Arabidopsis root quiescent center. Plant Cell 17: 1908–1925.

Nilsson, L., R. Müller and T.H. Nielsen (2007) Increased expression of the MYB-related transcription factor, *PHR1*, leads to enhanced phosphate uptake in *Arabidopsis thaliana*. Plant Cell Environ. 30: 1499–1512.

Nilsson, L., R. Müller and T.H. Nielsen (2010) Dissecting the plant transcriptome and the regulatory responses to phosphate deprivation. Physiol. Plant. 139: 129–143.

Nishida, S., Y. Kakei, Y. Shimada and T. Fujiwara (2017) Genome wide analysis of specific alterations in transcript structure and accumulation caused by nutrient deficiencies in *Arabidopsis thaliana*. Plant J. 91: 741–753.

Niu, Y.F., R.S. Chai, G.L. Jin, H. Wang, C.X. Tang and Y.S. Zhang (2013) Responses of root architecture development to low phosphorus availability: a review. Ann. Bot. 112: 391–408.

Obayashi, T. and K. Kinoshita (2010) Coexpression landscape in ATTED-II: usage of gene list and gene network for various types of pathways. J. Plant Res. 123: 311–319.

Obayashi, T., K. Nishida, K. Kasahara and K. Kinoshita (2011) ATTED-II updates: condition-specific gene coexpression to extend coexpression analyses and applications to a broad range of flowering plants. Plant Cell Physiol. 52: 213–219.

Okada, T., H. Nakayama, A. Shinmyo and K. Yoshida (2008) Expression of *OsHAK* genes encoding potassium ion transporters in rice. Plant Biotechnol. 25: 241–245.

Oono, Y., Y. Kawahara, T. Yazawa, H. Kanamori, M. Kuramata, H. Yamagata, S. Hosokawa, H. Minami, S. Ishikawa, J. Wu *et al.* (2013) Diversity in the complexity of phosphate starvation transcriptomes among rice cultivars based on RNA-Seq profiles. Plant Mol. Biol. 83: 523–537.

Pagnussat, G.C., M. Simontacchi, S. Puntarulo and L. Lamattina (2002) Nitric oxide is required for root organogenesis. Plant Physiol. 129: 954–956.

Pagnussat, G.C., M.L. Lanteri and L. Lamattina (2003) Nitric oxide and cyclic GMP are messengers in the indore acetic acid-induced adventitious rooting process. Plant Physiol. 132: 1241–1248.

Pariasca-Tanaka, J., K. Satoh, T. Rose, R. Mauleon and M. Wissuwa (2009) Stress response versus stress tolerance: a transcriptome analysis of two rice lines contrasting in tolerance to phosphorus deficiency. Rice (N Y) 2: 167–185.

Park, M.R., S.H. Baek, B.G. de Los Reyes, S.J. Yun and K.H.

Hasenstein (2012) Transcriptome profiling characterizes phosphate deficiency effects on carbohydrate metabolism in rice leaves. J. Plant Physiol. 169: 193–205.

Paszkowski, U., S. Kroken, C. Roux and S.P. Briggs (2002) Rice phosphate transporters include an evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis. Proc. Natl. Acad. Sci. USA 99: 13324–13329.

Petryszak, R., M. Keays, Y.A. Tang, N.A. Fonseca, E. Barrera, T. Burdett, A. Füllgrabe, A.M. Fuentes, S. Jupp, S. Koskinen *et al.* (2016) Expression Atlas update—an integrated database of gene and protein expression in humans, animals and plants. Nucleic Acids Res. 44: D746–D752.

Plaxton, W.C. and H.T. Tran (2011) Metabolic adaptations of phosphate-starved plants. Plant Physiol. 156: 1006–1015.

Poirier, Y. and M. Bucher (2002) Phosphate transport and homeostasis in Arabidopsis. Arabidopsis Book 1: e0024.

Ray, D.K., N.D. Mueller, P.C. West and J.A. Foley (2013) Yield trends are insufficient to double global crop production by 2050. PLoS ONE 8: e66428.

Rouached, H., A.B. Arpat and Y. Poirier (2010) Regulation of phosphate starvation responses in plants: signaling players and cross-talks. Mol. Plant 3: 288–299.

Rubio, V., F. Linhares, R. Solano, A.C. Martin, J. Iglesias, A. Leyva and J. Paz-Ares (2001) A conserved MYB transcription factor involved in phosphate starvation signaling both in vascular plants and in unicellular algae. Genes Dev. 15: 2122–2133.

Sato, Y., B.A. Antonio, N. Namiki, H. Takehisa, H. Minami, K. Kamatsuki, K. Sugimoto, Y. Shimizu, H. Hirochika and Y. Nagamura (2011a) RiceXPro: a platform for monitoring gene expression in *japonica* rice grown under natural field conditions. Nucleic Acids Res. 39: D1141–D1148.

Sato, Y., B. Antonio, N. Namiki, R. Motoyama, K. Sugimoto, H. Takehisa, H. Minami, K. Kamatsuki, M. Kusaba, H. Hirochika *et al.* (2011b) Field transcriptome revealed critical developmental and physiological transitions involved in the expression of growth potential in *japonica* rice. BMC Plant Biol. 11: 10.

Sato, Y., H. Takehisa, K. Kamatsuki, H. Minami, N. Namiki, H. Ikawa, H. Ohyanagi, K. Sugimoto, B.A. Antonio and Y. Nagamura (2013a) RiceXPro Version 3.0: expanding the informatics resource for rice transcriptome. Nucleic Acids Res. 41: D1206–D1213.

Sato, Y., N. Namiki, H. Takehisa, K. Kamatsuki, H. Minami, H. Ikawa, H. Ohyanagi, K. Sugimoto, J.I. Itoh, B.A. Antonio *et al.* (2013b) RiceFREND: a platform for retrieving coexpressed gene networks in rice. Nucleic Acids Res. 41: D1214–D1221.

Secco, D., M. Jabnoune, H. Walker, H. Shou, P. Wu, Y. Poirier and J. Whelan (2013) Spatio-temporal transcript profiling of rice roots and shoots in response to phosphate starvation and recovery. Plant Cell 25: 4285–4304.

Shaik, R. and W. Ramakrishna (2013) Genes and co-expression modules common to drought and bacterial stress responses in Arabidopsis and rice. PLoS ONE 8: e77261.

Sharma, R., G. Singh, S. Bhattacharya and A. Singh (2018) Comparative transcriptome meta-analysis of *Arabidopsis thaliana* under drought and cold stress. PLoS ONE 13: e0203266.

Shukla, D., C.A. Rinehart and S.V. Sahi (2017) Comprehensive study of excess phosphate response reveals ethylene mediated signaling that negatively regulates plant growth and development. Sci. Rep. 7: 3074.

Sinha, S.K., V.A.M. Sevanthi, S. Chaudhary, P. Tyagi, S. Venkadesan, M. Rani and P.K. Mandal (2018) Transcriptome analysis of two rice varieties contrasting for nitrogen use efficiency under chronic N starvation reveals differences in chloroplast and starch metabolism-related genes. Genes (Basel) 9: 206.

Sonoda, Y., A. Ikeda, S. Saiki, N. von Wirén, T. Yamaya and J. Yamaguchi (2003) Distinct expression and function of three ammonium transporter genes (*OsAMT1;1-1;3*) in rice. Plant Cell Physiol. 44: 726–734.

Sparks, D.L. and P.M. Huang (1985) Physical chemistry of soil potassium. *In*: Munson, R.D. (ed.) Potassium in agriculture, ASA, CSSA and SSSA, Madison, pp. 201–276.

Suenaga, A., K. Moriya, Y. Sonoda, A. Ikeda, N. von Wiren, T. Hayakawa, J. Yamaguchi and T. Yamaya (2003) Constitutive expression of a novel-type ammonium transporter *OsAMT2* in rice plants. Plant Cell Physiol. 44: 206–211.

Sun, H., J. Tao, S. Liu, S. Huang, S. Chen, X. Xie, K. Yoneyama, Y. Zhang and G. Xu (2014) Strigolactones are involved in phosphate- and nitrate-deficiency-induced root development and auxin transport in rice. J. Exp. Bot. 65: 6735–6746.

Sun, H., Y. Bi, J. Tao, S. Huang, M. Hou, R. Xue, Z. Liang, P. Gu, K. Yoneyama, X. Xie *et al.* (2016) Strigolactones are required for nitric oxide to induce root elongation in response to nitrogen and phosphate deficiencies in rice. Plant Cell Environ. 39: 1473–1484.

Tabuchi, M., K. Sugiyama, K. Ishiyama, E. Inoue, T. Sato, H. Takahashi and T. Yamaya (2005) Severe reduction in growth rate and grain filling of rice mutants lacking OsGS1;1, a cytosolic glutamine synthetase1;1. Plant J. 42: 641–651.

Tabuchi, M., T. Abiko and T. Yamaya (2007) Assimilation of ammonium ions and reutilization of nitrogen in rice (*Oryza sativa* L.). J. Exp. Bot. 58: 2319–2327.

Takehisa, H., Y. Sato, M. Igarashi, T. Abiko, B.A. Antonio, K. Kamatsuki, H. Minami, N. Namiki, Y. Inukai, M. Nakazono *et al.* (2012) Genome-wide transcriptome dissection of the rice root system: implications for developmental and physiological functions. Plant J. 69: 126–140.

Takehisa, H., Y. Sato, B.A. Antonio and Y. Nagamura (2013) Global transcriptome profile of rice root in response to essential macronutrient deficiency. Plant Signal. Behav. 8: e24409.

Takehisa, H., Y. Sato, B. Antonio and Y. Nagamura (2015) Coexpression network analysis of macronutrient deficiency response genes in rice. Rice (N Y) 8: 24.

Takehisa, H. (2019) Rice gene expression resources for elucidating response to nutritional environment and improving crop production. Breed. Res. 21: 41–46 (in Japanese).

Takehisa, H. and Y. Sato (2019) Transcriptome monitoring visualizes growth stage-dependent nutrient status dynamics in rice under field conditions. Plant J. 97: 1048–1060.

Tamura, W., Y. Hidaka, M. Tabuchi, S. Kojima, T. Hayakawa, T. Sato, M. Obara, M. Kojima, H. Sakakibara and T. Yamaya (2010) Reverse genetics approach to characterize a function of NADH-glutamate synthase1 in rice plants. Amino Acids 39: 1003–1012.

Tamura, W., S. Kojima, A. Toyokawa, H. Watanabe, M. Tabuchi-Kobayashi, T. Hayakawa and T. Yamaya (2011) Disruption of a novel NADH-glutamate synthase2 gene caused marked reduction in spikelet number of rice. Front. Plant Sci. 2: 57.

Tang, Z., X. Fan, Q. Li, H. Feng, A.J. Miller, Q. Shen and G. Xu (2012) Knockdown of a rice stelar nitrate transporter alters long-distance translocation but not root influx. Plant Physiol. 160: 2052–2063.

Tyagi, W. and M. Rai (2017) Root transcriptomes of two acidic soil adapted Indica rice genotypes suggest diverse and complex mechanism of low phosphorus tolerance. Protoplasma 254: 725–736.

Umehara, M., A. Hanada, H. Magome, N. Takeda-Kamiya and S. Yamaguchi (2010) Contribution of strigolactones to the inhibition of tiller bud outgrowth under phosphate deficiency in rice. Plant Cell Physiol. 51: 1118–1126.

Vance, C.P., C. Uhde-Stone and D.L. Allan (2003) Phosphorus

acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol. 157: 423–447.

Wada, S., Y. Hayashida, M. Izumi, T. Kurusu, S. Hanamata, K. Kanno, S. Kojima, T. Yamaya, K. Kuchitsu, A. Makino *et al.* (2015) Autophagy supports biomass production and nitrogen use efficiency at the vegetative stage in rice. Plant Physiol. 168: 60–73.

Wang, C., S. Ying, H. Huang, K. Li, P. Wu and H. Shou (2009a) Involvement of *OsSPX1* in phosphate homeostasis in rice. Plant J. 57: 895–904.

Wang, C., W. Huang, Y. Ying, S. Li, D. Secco, S. Tyerman, J. Whelan and H. Shou (2012) Functional characterization of the rice *SPX-MFS* family reveals a key role of *OsSPX-MFS1* in controlling phosphate homeostasis in leaves. New Phytol. 196: 139–148.

Wang, R., K. Guegler, S.T. LaBrie and N.M. Crawford (2000) Genomic analysis of a nutrient response in Arabidopsis reveals diverse expression patterns and novel metabolic and potential regulatory genes induced by nitrate. Plant Cell 12: 1491–1509.

Wang, R., M. Okamoto, X. Xing and N.M. Crawford (2003) Microarray analysis of the nitrate response in Arabidopsis roots and shoots reveals over 1,000 rapidly responding genes and new linkages to glucose, trehalose-6-phosphate, iron, and sulfate metabolism. Plant Physiol. 132: 556–567.

Wang, W., B. Hu, D. Yuan, Y. Liu, R. Che, Y. Hu, S. Ou, Y. Liu, Z. Zhang, H. Wang *et al.* (2018a) Expression of the nitrate transporter gene *OsNRT1.1A*/*OsNPF6.3* confers high yield and early maturation in rice. Plant Cell 30: 638–651.

Wang, Y.Y., Y.H. Cheng, K.E. Chen and Y.F. Tsay (2018b) Nitrate transport, signaling and use efficiency. Annu. Rev. Plant Biol. 69: 85–122.

Wang, Z., H. Hu, H. Huang, K. Duan, Z. Wu and P. Wu (2009b) Regulation of OsSPX1 and OsSPX3 on expression of *OsSPX* domain genes and Pi-starvation signaling in rice. J. Integr. Plant Biol. 51: 663–674.

Wasaki, J., R. Yonetani, S. Kuroda, T. Shinano, J. Yazaki, F. Fujii, K. Shimbo, K. Yamamoto, K. Safkata, T. Sasaki *et al.* (2003) Transcriptomic analysis of metabolic changes by phosphorus stress in rice plant roots. Plant Cell Environ. 26: 1515–1523.

Wasaki, J., T. Shinano, K. Onishi, R. Yonetani, J. Yazaki, F. Fujii, K. Shimbo, M. Ishikawa, Z. Shimatani, Y. Nagata *et al.* (2006) Transcriptomic analysis indicates putative metabolic changes caused by manipulation of phosphorus availability in rice leaves. J. Exp. Bot. 57: 2049–2059.

Woll, K., L.A. Borsuk, H. Stransky, D. Nettleton, P.S. Schnable and F. Hochholdinger (2005) Isolation, characterization, and pericycle-specific transcriptome analyses of the novel maize lateral and seminal root initiation mutant *rum1*. Plant Physiol. 139: 1255–1267.

Woo, J., C.R. MacPherson, J. Liu, H. Wang, T. Kiba, M.A. Hannah, X.J. Wang, V.B. Bajic and N.H. Chua (2012) The response and recovery of the *Arabidopsis thaliana* transcriptome to phosphate starvation. BMC Plant Biol. 12: 62.

Xia, L., D. Zou, J. Sang, X. Xu, H. Yin, M. Li, S. Wu, S. Hu, L. Hao and Z. Zhang (2017) Rice Expression Database (RED): an integrated RNA-Seq-derived gene expression database for rice. J. Genet. Genomics 44: 235–241.

Xia, X., X. Fan, J. Wei, H. Feng, H. Qu, D. Xie, A.J. Miller and G. Xu (2015) Rice nitrate transporter OsNPF2.4 functions in low-affinity acquisition and long-distance transport. J. Exp. Bot. 66: 317–331.

Xin, W., L. Zhang, W. Zhang, J. Gao, J. Yi, X. Zhen, M. Du, Y. Zhao and L. Chen (2019a) An integrated analysis of the rice transcriptome and metabolome reveals root growth regulation mechanisms in response to nitrogen availability. Int. J. Mol. Sci. 20: 5893.

Xin, W., L. Zhang, W. Zhang, J. Gao, J. Yi, X. Zhen, Z. Li, Y. Zhao, C. Peng and C. Zhao (2019b) An integrated analysis of the rice transcriptome and metabolome reveals differential regulation of carbon and nitrogen metabolism in response to nitrogen availability. Int. J. Mol. Sci. 20: 2349.

Xu, J., H.D. Li, L.Q. Chen, Y. Wang, L.L. Liu, L. He and W.H. Wu (2006) A protein kinase, interacting with two calcineurin B-like proteins, regulates K^+ transporter AKT1 in *Arabidopsis*. Cell 125: 1347–1360.

Xuan, W., T. Beeckman and G. Xu (2017) Plant nitrogen nutrition: sensing and signaling. Curr. Opin. Plant Biol. 39: 57–65.

Yan, M., X.R. Fan, H.M. Feng, A.J. Miller, Q.R. Shen and G.H. Xu (2011) Rice OsNAR2.1 interacts with OsNRT2.1, OsNRT2.2 and OsNRT2.3a nitrate transporters to provide uptake over high and low concentration ranges. Plant Cell Environ. 34: 1360–1372.

Yang, H.C., C.C. Kan, T.H. Hung, P.H. Hsieh, S.Y. Wang, W.Y. Hsieh and M.H. Hsieh (2017) Identification of early ammonium nitrate-responsive genes in rice roots. Sci. Rep. 7: 16885.

Yang, S.Y., D.L. Hao, Z.Z. Song, G.Z. Yang, L. Wang and Y.H. Su (2015a) RNA-Seq analysis of differentially expressed genes in rice under varied nitrogen supplies. Gene 555: 305–317.

Yang, T., S. Zhang, Y. Hu, F. Wu, Q. Hu, G. Chen, J. Cai, T. Wu, N. Moran, L. Yu *et al.* (2014) The role of a potassium transporter OsHAK5 in potassium acquisition and transport from roots to shoots in rice at low potassium supply levels. Plant Physiol. 166: 945–959.

Yang, W., J. Yoon, H. Choi, Y. Fan, R. Chen and G. An (2015b) Transcriptome analysis of nitrogen-starvation-responsive genes in rice. BMC Plant Biol. 15: 31.

Yu, P., K. Eggert, N. von Wirén, C. Li and F. Hochholdinger (2015) Cell type-specific gene expression analyses by RNA sequencing reveal local high nitrate-triggered lateral root initiation in shoot-borne roots of maize by modulating auxin-related cell cycle regulation. Plant Physiol. 169: 690–704.

Yu, P., J.A. Baldauf, A. Lithio, C. Marcon, D. Nettleton, C. Li and F. Hochholdinger (2016) Root type-specific reprogramming of maize pericycle transcriptomes by local high nitrate results in disparate lateral root branching patterns. Plant Physiol. 170: 1783–1798.

Zhang, J., L. Xu, F. Wang, M. Deng and K. Yi (2012) Modulating the root elongation by phosphate/nitrogen starvation in an OsGLU3 dependant way in rice. Plant Signal. Behav. 7: 1144–1145.

Zhang, Q., C. Wang, J. Tian, K. Li and H. Shou (2011) Identification of rice purple acid phosphatases related to phosphate starvation signalling. Plant Biol. (Stuttg) 13: 7–15.

Zhang, X., H. Jiang, H. Wang, J. Cui, J. Wang, J. Hu, L. Guo, Q. Qian and D. Xue (2017) Transcriptome analysis of rice seedling roots in response to potassium deficiency. Sci. Rep. 7: 5523.

Zhao, S., M.L. Zhang, T.L. Ma and Y. Wang (2016) Phosphorylation of ARF2 relieves its repression of transcription of the K^+ transporter gene *HAK5* in response to low potassium stress. Plant Cell 28: 3005–3019.

Zhou, J., F. Jiao, Z. Wu, Y. Li, X. Wang, X. He, W. Zhong and P. Wu (2008) *OsPHR2* is involved in phosphate-starvation signaling and excessive phosphate accumulation in shoots of plants. Plant Physiol. 146: 1673–1686.

Zhu, M., H. Xie, X. Wei, K. Dossa, Y. Yu, S. Hui, G. Tang, X. Zeng, Y. Yu, P. Hu *et al.* (2019) WGCNA analysis of salt responsive core transcriptome identifies novel hub genes in rice. Genes (Basel) 10: 719.