Invited Review

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

Hinako Takehisa and Yutaka Sato*

Institute of Crop Science, National Agriculture and Food Research Organization, 2-1-2 Kannondai, Tsukuba, Ibaraki 305-8518, Japan

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 | Treatment | Nutrient form | Treatment period | Tissue | Stage | Cultivar | Tool | Reference |
|----------|-----------|---------------|------------------|--------|-------|----------|------|-----------|
| N        | +N        | (NH₄)₂SO₄     | 3 h              | root   | 17 day seedling | Dongjin (J) | microarray | Chandran et al. 2016 |
|          | –N        | NH₄NO₃       | 1 h              | root   | 10 day seedling | TNG67 (J) | microarray | Hsieh et al. 2018 |
|          | Low N     | NH₄NO₃       | 20 min, 1, 2 h   | root, shoot | four-leaf stage | Minghui 63 (I) | microarray | Lian et al. 2006 |
|          | Low N     | NH₄NO₃       | 15 d             | root, shoot | 15 day seedling | IR64 (I), Nagina 22 (I) | RNA-seq | Sinha et al. 2018 |
|          | Low N, High N | NH₄NO₃     | 30 d             | root three-leaf stage | Shemong265 (J) | RNA-seq | Xin et al. 2019a |
|          | Low N, High N | NH₄NO₃     | 30 d             | leaf three-leaf stage | Shemong265 (J) | RNA-seq | Xin et al. 2019b |
|          | –N, High N | (NH₄)₂SO₄     | 4 h              | root, shoot | 10 day seedling | Nipponbare (J) | RNA-seq | Yang et al. 2015a |
|          | Low N     | NH₄NO₃       | 12 h             | root, leaf sheath six-leaf stage | Dongjin (J) | RNA-seq | Yang et al. 2015b |
|          | –N        | NH₄NO₃       | 30 min           | root | 17 day seedling | TNG67(J) | microarray | Yang et al. 2017 |
| P        | Low P     | NaH₂PO₄      | 6, 24 h, 2, 3 d  | seedling | 7 day seedling | Zhonghua 10 (J) | microarray | Dai et al. 2012 |
|          | Low P     | NaH₂PO₄      | 9 d              | leaf root | 15 day seedling | Dongxiang (W) | RNA-seq | Deng et al. 2018 |
|          | Low P     | NaH₂PO₄      | 6, 24 h, 3 d     | root | four-leaf stage | Zhongzaol8 (I), Lagne (I) | microarray | Li et al. 2010 |
|          | Low P     | NaH₂PO₄      | 15 d             | root, shoot | 2 day seedling | Dular (I), PB1(I) | microarray | Mehta et al. 2016 |
|          | Low P     | NaH₂PO₄      | 10, 22 d         | root, shoot | 14 day seedling | Nipponbare (J), IAC 25 (J) | RNA-seq | Oono et al. 2013 |
|          | –P        | NaH₂PO₄      | 40 d             | root, shoot | seed | Nipponbare (J), NIL (Pup I) | microarray | Pariasca-Tanaka et al. 2009 |
|          | –P, +P    | NaH₂PO₄      | 5 d              | leaf | three-leaf stage | Dongjin byeo (J) | microarray | Park et al. 2012 |
|          | –P        | NaH₂PO₄      | 1, 6, 24 h, 3, 7 d, 21 d (-P) | root, shoot | 14 day seedling | Nipponbare (J) | RNA-seq | Secco et al. 2013 |
|          | –P        | NaH₂PO₄      | 5 d              | leaf | 7 day seedling | Michikogane (J) | microarray | Wasaki et al. 2003 |
|          | –K        | K₂SO₄        | 6 h, 3, 5 d      | root | 14 day seedling | Nipponbare (J) | microarray | Wasaki et al. 2006 |
|          | –K        | K₂SO₄        | 1, 9 d           | root | 7 day seedling | Michikogane (J) | microarray | Ma et al. 2012 |
|          | Low K     | K₂SO₄        | 24 h, 2, 4 d     | root three-leaf stage | Nipponbare (J) | RNA-seq | Zhang et al. 2017 |
| NPK      | –N, –P, –K | NH₄NO₃, NaH₂PO₄, K₂SO₄ | 6, 24 h | root | 7 day seedling | Nipponbare (J) | microarray | Takehisa et al. 2013 |
|          | Low N, P, K | NH₄NO₃, NaH₂PO₄, K₂SO₄ | 5 d | shoot | 7 day seedling | Nipponbare (J) | microarray | Takehisa et al. 2015 |
|          | High N, P, K | NH₄NO₃, NaH₂PO₄, K₂SO₄ | 5 d | shoot | 7 day seedling | Nipponbare (J) | microarray | Takehisa and Sato 2019 |

*a: –N: N-free, –P: P-free, –K: K-free, +N: recovery N after deficiency, +P: recovery P after deficiency.

Note: 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 (Guibouleau 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...
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/PHOS81/XPR1) domain genes (SPXs), phosphate transporters (PTs/PHTs), purple acid phosphatases (PAPs), INDUCED BY PHOSPHATE STARVATION 1 (IPS1) (Bari et al. 2006, Bustos et al. 2010, Nilsson et al. 2007, Rubio et al. 2001), and miRNAs (Kuo and Chio 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, Chio 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 (LTI) (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,
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, RC13, 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).

### Response to potassium

### 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](image.png)

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 (Lanquart 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), RiceFRENDS (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.
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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