



# A curated list of genes that affect the plant ionome

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## Abstract

Understanding the mechanisms underlying plants' adaptation to their environment will require knowledge of the genes and alleles underlying elemental composition. Modern genetics is capable of quickly, and cheaply indicating which regions of DNA are associated with particular phenotypes in question, but most genes remain poorly annotated, hindering the identification of candidate genes. To help identify candidate genes underlying elemental accumulations, we have created the known ionome gene (KIG) list: a curated collection of genes experimentally shown to change uptake, accumulation, and distribution of elements. We have also created an automated computational pipeline to generate lists of KIG orthologs in other plant species using the PhytoMine database. The current version of KIG consists of 176 known genes covering 5 species, 23 elements, and their 1588 orthologs in 10 species. Analysis of the known genes demonstrated that most were identified in the model plant *Arabidopsis thaliana*, and that transporter coding genes and genes altering the accumulation of iron and zinc are overrepresented in the current list.

## KEYWORDS

curated, ionomics, mineral nutrition

## 1 | INTRODUCTION

Understanding the complex relationships that determine plant adaptation will require detailed knowledge of the action of individual genes, the environment, and their interactions. One of the fundamental processes that plants must accomplish is to manage the uptake, distribution, and storage of elements from the environment. Many different physiological, chemical, biochemical, and cell biology processes are involved in moving elements, implicating thousands of genes in every plant species. Modern genetic techniques have made it easy and inexpensive to identify hundreds to thousands of loci for traits, such as the elemental composition (or ionome) of plant tissues. However, moving from loci to genes is still

difficult as the number of possible candidates is often extremely large and the ability of researchers to identify a candidate gene from its functional annotations is limited by our current knowledge and inherent biases about what is worth studying (Stoeger et al., 2018; Baxter, 2020).

The most obvious candidates for genes affecting the ionome in a species are orthologs of genes that have been shown to affect elemental accumulation in another species. Indeed, there are multiple examples of orthologs affecting elemental accumulation in distantly related species, such as *Arabidopsis thaliana* and rice (*Oryza sativa*), including Na<sup>+</sup> transporters from the HKT family (Ren et al., 2005; Baxter et al., 2010); the heavy metal transporters AtHMA3 and OsHMA3 (Chao et al., 2012; Yan et al., 2016); E3

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ubiquitin ligase BRUTUS and OsHRZs that regulate the degradation of iron uptake factors (Selote et al., 2015; Hindt et al., 2017; Kobayashi et al., 2013) and the K<sup>+</sup> channel AKT1 (Ahmad et al., 2016; Lagarde et al., 1996). To our knowledge, no comprehensive list of genes known to affect elemental accumulation in plants exists. To ameliorate this deficiency, we sought to create a curated list of genes based on peer-reviewed literature along with a pipeline to identify orthologs of the genes in any plant species and a method for continuously updating the list. Here we present version 1.0 of the known ionome gene (KIG) list.

## 2 | MATERIALS AND METHODS

The list includes all functionally characterized genes from the literature that are linked to changes in the ionome. Criteria for inclusion in the primary KIG list were as follows:

1. The function or levels of the gene are unambiguously altered (i.e., a confirmed knockout, knockdown or overexpressor). For double mutants, both genes are listed.
2. The levels of at least one element are significantly altered in plant tissue.
3. Publication in the form of a peer-reviewed manuscript.

Note that our definition excludes genes that are linked to metal tolerance or sensitivity but do not alter the ionome, or genes where the levels of the transcript are correlated with elemental accumulation. In order to identify the KIG genes, we created a Google survey that was distributed to members of the Ionomichub research coordination network (NSF DBI-0953433), as well as advertising on Twitter and in oral presentations by the authors. We asked submitters to provide the species, gene name (or names where alleles of two genes were required for a phenotype), gene ID(s), tissue(s), element(s) altered, and a DOI link for the primary literature support. Subsequently, authors FKR and LW did an extensive literature search.

### 2.1 | Creating the inferred orthologs list

The known ionome gene list contains known genes from the primary list and their orthologous genes inferred by InParanoid (v4.1) pairwise species comparisons (Remm et al., 2001). The InParanoid files were downloaded from Phytozome for each organism-to-organism combination of species in the primary list, plus *Glycine max*, *Sorghum bicolor*, *Setaria italica*, *Setaria viridis*, and *Populus trichocarpa*. Orthologs of the primary genes were labeled as “inferred” genes. If a primary gene was also found as an ortholog to a primary gene in another species, the status was changed to “Primary/Inferred” in both species. It is important to note that only primary genes can infer genes; inferred genes cannot infer other genes. The pipeline for transforming the primary list into the known ionomics gene list can be found at <https://github.com/baxterlab/KIG>.

### 2.2 | Gene Enrichment analysis

Overrepresentation analysis (released July 11, 2019) was performed on the primary and inferred genes in *A. thaliana* using the GO Consortium's web-based GO Enrichment Analysis tool powered by the PANTHER (v14) classification system tool (Ashburner et al., 2000; Mi et al., 2017; The Gene Ontology Consortium, 2017). We restricted overrepresentation analysis to *A. thaliana* because of its dominance in the KIG list and our lack of confidence in the functional annotation of the other species on the list. An analysis performed by Wimalanathan et al. (2018) found that maize gene annotations in databases like Gramene and Phytozome lacked GO annotations outside of automatically assigned, electronic annotations (IEA). IEA annotations are not curated and have the least amount of support out of all the evidence codes (Harris et al., 2004). *A. thaliana* annotations come from a variety of evidence types, showing a higher degree of curation compared to maize (Wimalanathan et al., 2018). The whole-genome *Arabidopsis thaliana* gene list from the PANTHER database was used as the reference list.

We tested both the PANTHER GO-slim and the GO complete datasets for biological processes, molecular function, and cellular component. GO-Slim datasets contain a selected subset of terms that give a broad summary of the gene list, whereas the complete dataset contains all the terms returned for a more detailed analysis. The enriched terms (fold enrichment >1 and with a false discovery rate <0.05) from the complete dataset were sorted into five specific categories relating to the ionome based annotation terms:

1. Ion homeostasis - terms include homeostasis, stress, detoxification, regulation of an ion
2. Ion transport - terms specifically state transport, export, import or localization of ion(s). Does not include hydrogen ion transport
3. Metal ion chelation - terms relating to phytochelatin, other chemical reactions or pathways of metal chelator synthesis
4. Response to ions—vaguely states response to ions, but does not have any parent annotation terms that offer any more clarification (ie. stress response). Broadly this is referring to any change in the state or activity of cell secretion, expression, movement, or enzyme production (Carbon et al., 2009)
5. Other transport—annotation stating the transfer of anything that is not an ion (glucose, peptides, etc.)

Genes may belong to more than one category, but if they belong to a parent and child term in the same category, they are only counted once.

## 3 | RESULTS

The current primary list (v1.0) consists of 176 genes from *A. thaliana*, *O. sativa*, *Medicago truncatula*, *Triticum aestivum*, and *Zea mays* with the majority coming from *A. thaliana* and *O. sativa* (Table 1, Figure 1).

**TABLE 1** Primary known ionome genes

Species	GeneID	GeneName	Elements	Tissue	Citation(s)
<i>A. thaliana</i>	AT1G01340	CNGC10	K, Ca, Mg	Roots, shoots	Guo et al. (2010)
<i>A. thaliana</i>	AT1G01580	FRO2	Fe	Root	Robinson et al. (1999)
<i>A. thaliana</i>	AT1G07600	MT1A	Cd, Zn, As	Shoots	Zimeri et al. (2005)
<i>A. thaliana</i>	AT1G08490	CPNIFS	Se, S	Roots, shoots	Van Hoewyk et al. (2005)
<i>A. thaliana</i>	AT1G12640	LPCAT1	P	Leaf	Kisko et al. (2018)
<i>A. thaliana</i>	AT1G14040	PHO1;H3	P	Shoots	Khan et al. (2014)
<i>A. thaliana</i>	AT1G14870	PCR2	Zn	Shoots	Song et al. (2010)
<i>A. thaliana</i>	AT1G18910	BTSL2	Fe, Mn, Zn	Leaf	Hindt et al. (2017)
<i>A. thaliana</i>	AT1G20110	FYVE1	Fe, Zn, Co, Mn	Root	Barberon et al. (2014)
<i>A. thaliana</i>	AT1G30270	CIPK23	K	Shoots	Xu et al. (2006)
<i>A. thaliana</i>	AT1G30400	ABCC1	Cd	Shoots	Park et al. (2012)
<i>A. thaliana</i>	AT1G30450	CCC	Ca, K, Na,S	seeds	McDowell et al. (2013)
<i>A. thaliana</i>	AT1G31885	NIP3;1	As	Shoots	Xu et al. (2015)
<i>A. thaliana</i>	AT1G32450	AtNRT1.5/ AtNPF7.3	K, NO <sub>3</sub> -	Shoots, Roots	Li et al. (2017)
<i>A. thaliana</i>	AT1G36370	AtMSA1	S, Se	Shoots	Huang, et al. (2016)
<i>A. thaliana</i>	AT1G56160	myb72	Fe, Cd, Zn, Co, Mo	Leaf	Palmer et al. (2013)
<i>A. thaliana</i>	AT1G56430	NAS4	Fe, Cd, Co, Mo	Leaf	Palmer et al. (2013)
<i>A. thaliana</i>	AT1G59870	PEN3	Cd	Shoots, roots	Kim et al. (2007)
<i>A. thaliana</i>	AT1G60960	AtIRT3	Fe	Roots	Lin et al. (2009)
<i>A. thaliana</i>	AT1G62180	AtAPR2	S, Se	Shoots	Loudet et al. (2007); Chao, et al. (2014)
<i>A. thaliana</i>	AT1G63440	AtHMA5	Cu	Shoots	Andrés-Colás et al. (2006)
<i>A. thaliana</i>	AT1G66240	AtAX1	Cu	Shoots	Shin et al. (2012)
<i>A. thaliana</i>	AT1G68320	MYB62	P	Roots, shoots	Devaiah et al. (2009)
<i>A. thaliana</i>	AT1G71200	AtCITF1	Cu	Shoots, Anthers	Yan et al. (2017)
<i>A. thaliana</i>	AT1G74770	BTSL1	Fe, Mn, Zn	Leaf	Hindt et al. (2017)
<i>A. thaliana</i>	AT1G76430	PHT1;9	P, As	Roots, shoots	Remy et al. (2012)
<i>A. thaliana</i>	AT1G80760	NIP6;1	B	Leaves,shoots	Tanaka et al. (2008)
<i>A. thaliana</i>	AT1G80830	AtNRAMP1	Mn	Shoots, roots	Cailliatte et al. (2010)
<i>A. thaliana</i>	AT2G01770	VIT1	Fe	Seed	Kim et al. (2006)
<i>A. thaliana</i>	AT2G01980	SOS1/NHX7	Na	Shoots	Shi et al. (2003)
<i>A. thaliana</i>	AT2G13540	ABH1	S	seeds	McDowell et al. (2013)
<i>A. thaliana</i>	AT2G16770	AtbZIP23	Zn	Shoots, roots	Assunção et al. (2010)
<i>A. thaliana</i>	AT2G19110	AtHMA4	Zn	Shoots, seeds	Hussain et al. (2004); Olsen et al. (2016)
<i>A. thaliana</i>	AT2G21045	AtHAC1	As	Shoots	Chao, et al. (2014)
<i>A. thaliana</i>	AT2G23150	AtNRAMP3	Fe, Mn, Zn	Shoots	Lanquar et al. (2010)
<i>A. thaliana</i>	AT2G23240	AtMT4b	Cu, Zn	Seeds	Ren et al. (2012)
<i>A. thaliana</i>	AT2G25680	MOT1	Mo	Leaf	Baxter, Muthukumar, et al., 2008; Baxter, Vitek, et al., 2008
<i>A. thaliana</i>	AT2G28160	FRU	Fe	Shoots	Yuan et al. (2008)
<i>A. thaliana</i>	AT2G28670	ESB1	Ca, Mn, Zn, Na, S, K, As, Se, Mo	Leaf	Baxter et al. (2009)
<i>A. thaliana</i>	AT2G32830	PHT1;5	P	Roots	Nagarajan et al. (2011)
<i>A. thaliana</i>	AT2G33770	PHO2	P	Roots, shoots	Liu et al. (2012)

(Continues)

TABLE 1 (Continued)

Species	GeneID	GeneName	Elements	Tissue	Citation(s)
<i>A. thaliana</i>	AT2G37430	ZAT11	Ni	Shoots	Liu et al. (2014)
<i>A. thaliana</i>	AT2G38460	FPN1	Co	Leaf	Morrissey et al. (2009)
<i>A. thaliana</i>	AT2G38940	PHT1;4	P	Roots, shoots	Shin et al. (2004)
<i>A. thaliana</i>	AT2G39450	AtMTP11	Mn	Shoots, roots	Peiter et al. (2007)
<i>A. thaliana</i>	AT2G42000	AtMT4a	Cu, Zn	Seeds	Ren et al. (2012)
<i>A. thaliana</i>	AT2G46430	CNGC3	K	Leaf	Gobert et al. (2006)
<i>A. thaliana</i>	AT2G46800	AtMTP1	Zn	Shoots	Desbrosses-Fonrouge et al. (2005)
<i>A. thaliana</i>	AT2G47160	BOR1	B	Shoots	Miwa et al. (2006)
<i>A. thaliana</i>	AT3G01310	VIH2	P	Shoots	Zhu et al. (2019)
<i>A. thaliana</i>	AT3G06060	TSC10a	Na, K, Rb, Mg, Ca, Fe, Mo	Leaf	Chao et al. (2011)
<i>A. thaliana</i>	AT3G06100	NIP7	As	NA	Lindsay and Maathuis (2016; Isayenkov and Maathuis (2008)
<i>A. thaliana</i>	AT3G08040	FRD3/MAN1	Mn	Leaf	Delhaize (1996)
<i>A. thaliana</i>	AT3G12750	AtZIP1	Mn	Roots	Milner et al. (2013)
<i>A. thaliana</i>	AT3G12820	myb10	Fe, Cd, Zn, Co, Mo	Leaf	Palmer et al. (2013)
<i>A. thaliana</i>	AT3G13320	CAX2	Mn, Fe, K, P	Seed	Connorton et al. (2012)
<i>A. thaliana</i>	AT3G13405	mir169a	N	Root	Zhao et al. (2011)
<i>A. thaliana</i>	AT3G14280		S	seeds	McDowell et al. (2013)
<i>A. thaliana</i>	AT3G15380	AtCTL1	Na, Fe, Zn, Mn, Mo	Shoots, Roots	Gao et al. (2017)
<i>A. thaliana</i>	AT3G18290	BTS	Fe, Zn, Mn	Leaf	Hindt et al. (2017)
<i>A. thaliana</i>	AT3G22890	AtATPS1	S	Shoos	Koprivova et al. (2013)
<i>A. thaliana</i>	AT3G23210	bHLH34	Fe	Root, shoot	Li et al. (2016)
<i>A. thaliana</i>	AT3G23430	PHO1	P	Shoots	Khan et al. (2014)
<i>A. thaliana</i>	AT3G43790	ZIFL2	Cs	Leaf	Remy et al. (2015)
<i>A. thaliana</i>	AT3G47640	PYE	Fe, Zn, Mn, Co	Root	Long et al. (2010)
<i>A. thaliana</i>	AT3G47950	AHA4	Na	Root	Vitart et al. (2001)
<i>A. thaliana</i>	AT3G51860	CAX3	P, K	Seed	Connorton et al. (2012)
<i>A. thaliana</i>	AT3G51895	SULTR3;1	S	Leaf	Cao et al. (2013)
<i>A. thaliana</i>	AT3G56970	bHLH38	Fe	Shoots	Yuan et al. (2008)
<i>A. thaliana</i>	AT3G56980	bHLH39	Fe	Shoots	Yuan et al. (2008)
<i>A. thaliana</i>	AT3G58060	AtMTP8	Mn	Shoots, seeds	Eroglu et al. (2016, Eroglu et al. (2017)
<i>A. thaliana</i>	AT3G58810	AtMTP3	Zn	Shoots	Arrivault et al. (2006)
<i>A. thaliana</i>	AT3G58970	MGT6	Mg	Roots, shoots	Mao et al. (2014)
<i>A. thaliana</i>	AT3G62270	BOR2	B	Shoots	Miwa et al. (2013)
<i>A. thaliana</i>	AT4G02780	GA1	Fe	Root	Wild et al. (2016)
<i>A. thaliana</i>	AT4G10310	AtHKT1;1	Na	Leaf	Baxter et al. (2010)
<i>A. thaliana</i>	AT4G10380	NIP5;1	B	Roots, shoots	Takano et al. (2006)
<i>A. thaliana</i>	AT4G13420	HAK5	Rb, Cs	Roots	Rubio et al. (2008; Qi et al. (2008)
<i>A. thaliana</i>	AT4G14410	bHLH104	Fe	Root, shoot	Li et al. (2016)
<i>A. thaliana</i>	AT4G16370	OPT3	Fe, Cd	Leaf	Zhai et al. (2014)
<i>A. thaliana</i>	AT4G19690	IRT1	Fe, Mn, Co, Cd, Zn	Root	Eide et al. (1996)

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TABLE 1 (Continued)

Species	GeneID	GeneName	Elements	Tissue	Citation(s)
<i>A. thaliana</i>	AT4G23100	GSH1	Cd, As	Shoots	Guo et al. (2008)
<i>A. thaliana</i>	AT4G24120	YSL1	Fe, Zn, Cu	NA	Waters et al. (2006)
<i>A. thaliana</i>	AT4G28610	AtPHR1	P	Shoots	Nilsson et al. (2007)
<i>A. thaliana</i>	AT4G30110	AtHMA2	Zn	Shoots, seeds	Hussain et al. (2004; Olsen et al. (2016)
<i>A. thaliana</i>	AT4G30120	AtHMA3	Cd, Zn	Leaf	Chao et al. (2012; Pita-Barbosa et al. (2019)
<i>A. thaliana</i>	AT4G33000	CBL10	K	Shoots	Ren et al. (2013)
<i>A. thaliana</i>	AT4G35040	AtbZIP19	Zn	Shoots, roots	Assunção et al. (2010)
<i>A. thaliana</i>	AT4G37270	HMA1	Zn	Shoots	Kim et al. (2009)
<i>A. thaliana</i>	AT5G02600	NaKR1	Na, K, Rb	Leaf	Tian et al. (2010)
<i>A. thaliana</i>	AT5G03455	ACR2	As, P	Roots, shoots	Dhankher et al. (2006)
<i>A. thaliana</i>	AT5G03570	FPN2	Co, Ni	Leaf	Morrissey et al. (2009); Schaaf et al. (2006)
<i>A. thaliana</i>	AT5G09690	MGT7	Mg	Shoots	Kamiya et al. (2012)
<i>A. thaliana</i>	AT5G13740	ZIF1	Zn, Fe	Shoots	Haydon et al. (2012)
<i>A. thaliana</i>	AT5G15070	VIH1	P	Shoots	Zhu et al. (2019)
<i>A. thaliana</i>	AT5G15410	CNGC2/DND1	Ca, Mg	seeds	McDowell et al. (2013)
<i>A. thaliana</i>	AT5G17290	APG5	Fe, Mn, Zn	Leaf, shoots, seeds	Pottier et al. (2019)
<i>A. thaliana</i>	AT5G18830	AtSPL7	Cu	Shoots, roots	Bernal et al. (2012)
<i>A. thaliana</i>	AT5G20650	COPT5	Cu	Shoots, roots, seeds	Klaumann et al. (2011)
<i>A. thaliana</i>	AT5G35410	SOS2	Na	Seeds	McDowell et al. (2013)
<i>A. thaliana</i>	AT5G42130	AtMf11	Fe	Leaves, shoots	Tarantino et al. (2011)
<i>A. thaliana</i>	AT5G43350	PHT1;1	P, As	Shoots	Shin et al. (2004; Catarecha et al. (2007)
<i>A. thaliana</i>	AT5G44070	PCS1	Zn, Cd, As	Leaf	Kühnlenz et al. (2016; Guo et al. (2008)
<i>A. thaliana</i>	AT5G53130	CNGC1	Pb	Leaf	Sunkar et al. (2000)
<i>A. thaliana</i>	AT5G53550	YSL3	Fe, Zn, Cu	NA	Waters et al. (2006)
<i>A. thaliana</i>	AT5G54680	ILR3	Cd, Co, Fe, Mn, Zn	Leaf	Rampey et al. (2006)
<i>A. thaliana</i>	AT5G54810	AtTSB1	Cd	Roots,shoots	Sanjaya et al. (2008)
<i>A. thaliana</i>	AT5G57620	AtMYB36	Li, B, Na, Mg, K, Ca, Mn, Fe, Co, Ni, Cu, Zn, Rb, Sr, Mo, Cd	Shoots	Kamiya et al. (2015)
<i>A. thaliana</i>	AT5G59030	COPT1	Cu	Seed, Leaf	Sancenón et al. (2004)
<i>A. thaliana</i>	AT5G64930	CPR5	K	Leaf	Borghi et al. (2011)
<i>A. thaliana</i>	AT5G67330	AtNRAMP3	Fe, Mn, Zn	Shoots	Lanquar et al. (2010)
<i>M. truncatula</i>	Medtr1g010270	MtMOT1.2	Mo	Nodules	Gil-Díez et al. (2018)
<i>M. truncatula</i>	Medtr3g088460	MtNramp1	Fe	Nodules	Tejada-Jiménez et al. (2015)
<i>M. truncatula</i>	Medtr3g464210	MtMOT1.3	Mo	Nodules	Tejada-Jiménez et al. (2017)
<i>M. truncatula</i>	Medtr4g019870	MtCOPT1	Cu	Nodules	Senovilla et al. (2018)
<i>M. truncatula</i>	Medtr4g064893	MtMTP2	Zn	Nodules	León-Mediavilla et al. (2018)
<i>M. truncatula</i>	Medtr4g083570	MtZIP6	Zn	Nodules	Abreu et al. (2017)
<i>O. sativa</i>	LOC_Os01g03914	OsMTP9	Mn	Shoots	Ueno et al. (2015)
<i>O. sativa</i>	LOC_Os01g20160	OsHKT1;5	Na	Leaf, shoots	Kobayashi et al. (2017)
<i>O. sativa</i>	LOC_Os01g45990	AKT1	K	NA	Ahmad, et al. (2016)

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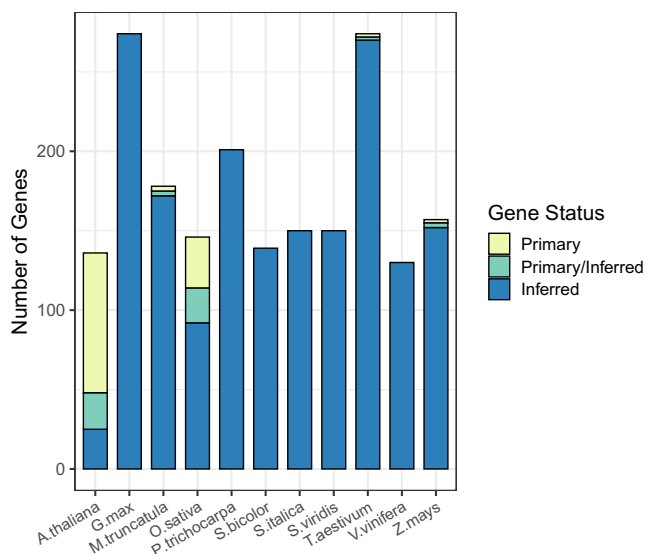
TABLE 1 (Continued)

Species	GeneID	GeneName	Elements	Tissue	Citation(s)
<i>O. sativa</i>	LOC_Os01g64250	OsHORZ1	Fe	Shoots,seeds	Kobayashi et al. (2013)
<i>O. sativa</i>	LOC_Os01g64890	OsMGT1	Mg,Na	Roots, shoots	Chen, et al. (2017)
<i>O. sativa</i>	LOC_Os02g06290	OsHAC4	As	Seed	Xu et al. (2017)
<i>O. sativa</i>	LOC_Os02g10290	OsHMA4	Cu	Roots, shoots, seeds	Huang, et al. (2016)
<i>O. sativa</i>	LOC_Os02g13870	OsNIP1;1	As	Shoots	Sun et al. (2018)
<i>O. sativa</i>	LOC_Os02g43370	OsYSL2	Fe, Mn	Seeds	Ishimaru et al. (2010)
<i>O. sativa</i>	LOC_Os02g43410	OsYSL15	Fe	Roots, shoots, seeds	Lee et al. (2009)
<i>O. sativa</i>	LOC_Os02g51110	LSI1	Se	Roots, shoots	Zhao et al. (2010)
<i>O. sativa</i>	LOC_Os02g53490	OsMTP8.2	Mn	Shoots, roots	Takemoto et al. (2017)
<i>O. sativa</i>	LOC_Os02g56510	OsPHO1;2	P	Shoots	Secco et al. (2010)
<i>O. sativa</i>	LOC_Os03g05640	OsPT2	Se	Roots, shoots	Zhang et al. (2014)
<i>O. sativa</i>	LOC_Os03g09140	OsRab6a	Fe, Zn	Seeds, shoot, roots	Yang and Zhang (2016)
<i>O. sativa</i>	LOC_Os03g12530	OsMTP8.1	Mn	Shoots, roots	Chen et al. (2013)
<i>O. sativa</i>	LOC_Os03g18550	OsMIT	Fe	Shoots	Bashir et al. (2011)
<i>O. sativa</i>	LOC_Os03g19420	OsNAS2	Fe	Seeds	Lee et al. (2012)
<i>O. sativa</i>	LOC_Os03g21240	OsPHR2	P	Shoots	Zhou et al. (2008)
<i>O. sativa</i>	LOC_Os04g32920	OsHAK1	Cs	Shoots, seeds	Rai et al. (2017)
<i>O. sativa</i>	LOC_Os04g38940	OsVIT1	Fe,Zn	Shoots, seeds	Zhang et al. (2012)
<i>O. sativa</i>	LOC_Os04g45860	OsYSL9	Fe	Shoots, seeds	Senoura et al. (2017)
<i>O. sativa</i>	LOC_Os04g45900	OsYSL16	Cu	Roots, shoots, seeds	Zheng et al. (2012)
<i>O. sativa</i>	LOC_Os04g46940	OsHMA5	Cu	Roots, shoots	Deng et al. (2013)
<i>O. sativa</i>	LOC_Os04g52310	OsZIP3	Zn	Shoots	Sasaki et al. (2015)
<i>O. sativa</i>	LOC_Os04g52900	OsABCC1	As	Seeds	Song et al. (2014)
<i>O. sativa</i>	LOC_Os04g56430	OsRMC	Fe,Mn,Cu	Root, shoot, seeds	Yang et al. (2013)
<i>O. sativa</i>	LOC_Os05g34290	OsPCS1*	As	Seeds	Hayashi et al. (2017)
<i>O. sativa</i>	LOC_Os05g39560	OsZIP5	Zn	Leaf	Lee et al. (2010)
<i>O. sativa</i>	LOC_Os05g47780	OsHRZ2	Fe	Shoots, seeds	Kobayashi et al. (2013)
<i>O. sativa</i>	LOC_Os05g48390	OsPHO2	P	Leaf	Wang et al. (2009)
<i>O. sativa</i>	LOC_Os06g01260	OsPCS2*	As, Cd	Seeds	Uraguchi et al. (2017)
<i>O. sativa</i>	LOC_Os06g05160	SPDT	P	Seed	Yamaji et al. (2017)
<i>O. sativa</i>	LOC_Os06g48720	OsHMA2	Zn	Shoots, roots	Takahashi et al. (2012)
<i>O. sativa</i>	LOC_Os06g48810	OsHKT2;1	Na	Roots, shoots	Horie et al. (2007)
<i>O. sativa</i>	LOC_Os07g01810	TPKb	K	Leaf, root	Ahmad et al. (2016)
<i>O. sativa</i>	LOC_Os07g09000	OsPHF1	P	Leaf, root	Chen et al. (2011)
<i>O. sativa</i>	LOC_Os07g12900	OsHMA3	Cd	Shoots, seeds	Tanaka et al. (2016)
<i>O. sativa</i>	LOC_Os07g15370	NRAMP5	Fe,Mn,Cd	Leaf	Sasaki et al. (2012)
<i>O. sativa</i>	LOC_Os08g01120	OsMOT1;1	Mo	Shoots, Seed	Huang et al. (2019)
<i>O. sativa</i>	LOC_Os08g04390	OsPRI1	Fe	Shoots, roots	Zhang et al. (2017)
<i>O. sativa</i>	LOC_Os08g05590	OsNIP3;2	As	Roots	Chen, Sun, et al. (2017a); Chen, Yamaji, et al. (2017b)
<i>O. sativa</i>	LOC_Os08g05600	OsNIP3;3	As	Shoots	Sun et al. (2018)
<i>O. sativa</i>	LOC_Os08g10480	OsATX1	Cu	Shoots, roots, seeds	Zhang, Cao, et al. (2018); Zhang, Chen, et al. (2018)

(Continues)

TABLE 1 (Continued)

Species	GeneID	GeneName	Elements	Tissue	Citation(s)
<i>O. sativa</i>	LOC_Os09g23300	OsVIT2	Fe, Zn	Shoots, seeds	Zhang et al. (2012)
<i>O. sativa</i>	LOC_Os12g03899	ZIFL12	Fe	Shoots	Che et al. (2019)
<i>O. sativa</i>	LOC_Os12g18410	OsMIR	Fe	Shoots, Roots, seeds	Ishimaru et al. (2009)
<i>O. sativa</i>	LOC_Os12g32400	OsBHLH133	Fe	Leaf, root, shoot	Wang, Sun, et al. (2013a); Wang, Ying, et al. (2013b)
<i>O. sativa</i>	LOC_Os12g37840	OsBOR1	B	Shoots	Nakagawa et al. (2007)
<i>O. sativa</i>	Os01g0689300	OsHRZ1	Fe	Shoots, seeds	Kobayashi et al. (2013)
<i>T. aestivum</i>	2AI-TRIAE_CS42_2AL_TGACv1_095050_AA410	TaIPK1	Fe, Zn	Seed	Aggarwal et al. (2018)
<i>T. aestivum</i>	Traes_4AS_7220D33B3	Ta-PHR1	P	Shoots	Wang, Sun, et al. (2013a); Wang, Ying, et al. (2013b)
<i>T. aestivum</i>	Traes_4BL_7091749BF	TaABCC13	Ca	Seed	Bhati et al. (2016)
<i>T. aestivum</i>	Traes_4DL_3F8034BFD	HKT2;1	Na	Roots	Laurie et al. (2002)
<i>Z. mays</i>	GRMZM2G047616	ZmHKT1	Na	Leaf	Zhang, Cao, et al. (2018); Zhang, Chen, et al. (2018)
<i>Z. mays</i>	GRMZM2G060952	YS1	Fe	Root	Von Wiren et al. (1994)
<i>Z. mays</i>	GRMZM2G063306	YS3	Fe	Leaf	Chan-Rodriguez and Walker (2018)
<i>Z. mays</i>	GRMZM2G084779	ZmHAK5	K	Roots, shoots	Qin et al. (2019)
<i>Z. mays</i>	GRMZM2G176209	TLS1	B	Shoots, roots, anthers	Durbak et al. (2014)



**FIGURE 1** Number of genes for each species that are primary, inferred from other primary genes in other species, or both

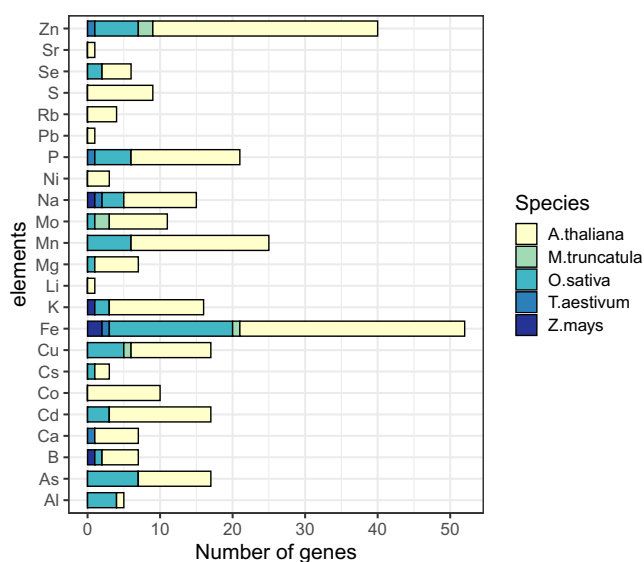
Most primary genes have orthologs in other species. Less than 10% of primary genes in *A. thaliana*, 12% in *O. sativa*, and one of the four primary genes in wheat (*T. aestivum*) lack orthologs (Table 2). *G. max*, *P. trichocarpa*, *S. bicolor*, *S. italica*, and *S. viridis* currently contain only inferred genes (Table 2, Figure 1).

The YSL genes in *A. thaliana* and *O. sativa* are an example that provides evidence for the validity of the KIG list pipeline: AtYSL3, OsYSL9, and OsYSL16 were listed in their respective species as primary genes (Table 1) and after the ortholog search was annotated as primary/inferred genes, referencing each other (Table S1). AtYSL2 in *A. thaliana*, was not listed as primary gene, but was inferred through its rice orthologs OsYSL9 and OsYSL16. Additionally, AtYSL1 in *A. thaliana* is not a paralog of AtYSL3 or an ortholog of OsYSL9 and OsYSL16 according to PhytoMine's InParanoid results and is not listed as an ortholog to either of the *O. sativa* YSL genes in the KIG list. Other examples include AtVIT1 and OsVIT1/OsVIT2 (Kim et al., 2006; Zhang et al., 2012), and the vacuolar Mn transporters AtMTP8 and OsMTP8 (Eroglu et al., 2016; Chen et al., 2013). Thus, we can reliably generate inferred genes and create a species-specific KIG list for any species in PhytoMine.

The primary list covers 23 elements (Figure 2) according to the reported elements from authors in the primary list, which is more elements than predicted by the GO term annotations for those genes. Some GO annotations for these genes mention only a portion of elements listed by the literature on the primary list. This may be due to GO annotation evidence codes lacking curation or biological data (IEA, ND, NAS) (Wimalanathan et al., 2018), or it may be due to alterations in one element leading to alterations in other elements (Baxter, Muthukumar, et al., 2008; Baxter, Vitek, et al., 2008).

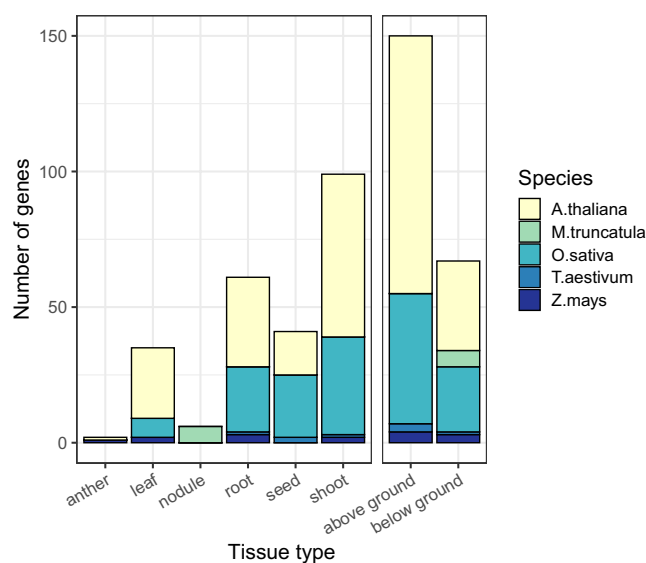
**TABLE 2** Break down of primary/inferred genes in each species

Species	Total genes	Primary genes	Primary/inferred genes	Inferred genes	Primary & primary/inferred genes without orthologs
<i>A. thaliana</i>	136	65.44%	16.18%	18.38%	9.91%
<i>O. sativa</i>	141	20.57%	14.89%	64.54%	12.00%
<i>M. truncatula</i>	176	1.70%	1.70%	96.59%	0.00%
<i>T. aestivum</i>	267	0.75%	0.75%	98.50%	25.00%
<i>Z. mays</i>	152	1.32%	1.97%	96.71%	0.00%
<i>G. max</i>	268	0.00%	0.00%	100.00%	0.00%
<i>P. trichocarpa</i>	197	0.00%	0.00%	100.00%	0.00%
<i>S. bicolor</i>	135	0.00%	0.00%	100.00%	0.00%
<i>S. italica</i>	146	0.00%	0.00%	100.00%	0.00%
<i>S. viridis</i>	146	0.00%	0.00%	100.00%	0.00%

**FIGURE 2** Number of primary genes from each species listing each element

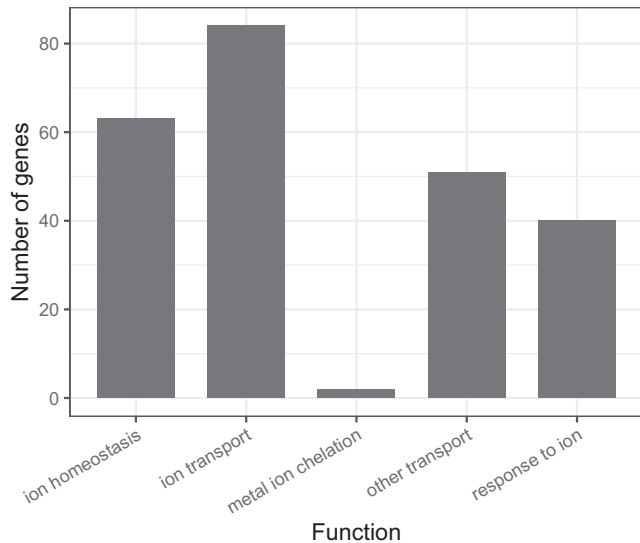
*A. thaliana* is the only species to have a primary gene listing for each element. There is a bias toward manganese, zinc, and iron which have two, three, and four times more associated genes than the average  $13 \pm 12$  genes of other elements. Iron is the only element to contain genes from all five species in the primary list. In addition to biases toward certain elements, our primary list is also skewed toward an overrepresentation of ionome genes in above-ground tissue studies (Figure 3). This is likely due to the difficulties in studying the elemental content of below-ground tissues. All *M. truncatula* genes come from studies of the nodule in this model legume species.

Querying the manually curated PANTHER GO-slim biological process database (PANTHER v14.1, released March 12, 2019) and the GO complete biological process database (GO Ontology database, released October 08, 2019) with the *A. thaliana* KIG genes returned significantly ( $FDR < 0.05$ ) overrepresented annotation terms related to the transport, response, and homeostasis of iron,

**FIGURE 3** Number of primary genes each type of tissue contributes to the known ionome gene list. Above ground is a summary of anther, leaf, seed, and shoot, while below ground is a summary of root and nodule

zinc, copper and manganese ions. Additionally, the GO complete results had terms for cadmium, nickel, cobalt, sulfur, arsenic, lead, selenium, boron, magnesium, phosphorus, sodium, potassium, and calcium; covering most of the elements in the KIG list (Figure 4). Even though some genes were annotated as associated in the “other transport” of glycoside, glucose, oligopeptides, or phloem transport, the citations that have added them into our primary list show that their mutant alleles altered elemental accumulation. *AtABCC1* is annotated as encoding a glycoside transporter protein, but Park et al. (2012) found overexpression of *AtABCC1* increased cadmium concentrations in shoot tissue. The *YSL* genes and *OPT3* are annotated as genes encoding oligopeptide transporters, but more specifically they are encoding predicted phloem-localized metal-nicotianamine complex and iron/cadmium transporters,





**FIGURE 4** Known ionome genes relating to different terms from the GO complete biological process dataset. Ontology groups of GO Enrichment Analysis from PANTHER

respectively (Waters et al., 2006; Zhai et al., 2014). Last, NRT1.5/NPF7.3 is also annotated as encoding an oligopeptide transporter, but Li et al., (2017) identified it as a xylem loading potassium ion antiporter.

The PANTHER GO-slim molecular function annotation database found a significant overrepresentation for iron and potassium cation transmembrane transporter activity in the *A. thaliana* genes. The results using the GO complete molecular function database supported this and additionally included terms for arsenic, cadmium, zinc, boron, manganese, phosphate, sulfur, and magnesium ion transmembrane transporter activity. The GO complete molecular database also returned overrepresented terms for metal ion-binding and cyclic nucleotide-binding annotations. The cyclic nucleotide-binding annotation genes were more specifically cyclic nucleotide ion gated channel genes (Gobert et al., 2006). The PANTHER GO-slim cell component and GO complete cell component annotation database both returned significant overrepresentation for vacuoles and the plasma membrane, both known to be critical for elemental movement and storage (Barkla & Pantoja, 1996). The molecular function and cell component results are further evidence that our list is dominated by ion transporters.

To test the completeness of the KIG list, we searched PANTHER's biological processes annotations for the number of *A. thaliana* genes encoding predicted elemental transporters. We found 618 *A. thaliana* genes predicted to encode elemental transport, and only 40 of these PANTHER genes are listed in the KIG list. We checked these results against ThaleMine (v1.10.4, updated on June 13, 2017) genes with the term "ion transport" in the gene name, description, or GO annotation and found only 358 genes, with 52 of these genes listed in the *A. thaliana* known ionome gene list. Interestingly, 219 of the genes from ThaleMine were not found in the 634 from PANTHER.

## 4 | DISCUSSION

Here we have produced a curated list of genes known to alter the elemental composition of plant tissues. We envision several possible uses for this list:

1. Researchers can use the list to identify candidate genes in loci from QTL and GWAS experiments.
2. This list can serve as a gold standard for computational approaches.
3. The list can serve as a reading list for those interested in learning about elemental accumulation.

It is important to highlight that the inferred genes lists are not likely to be perfect predictors of the causal genes. Our use of InParanoid orthologs may exclude homologs that are likely candidates. Additionally, the reasons that some genes have been studied could be the result of human bias toward research topics (Baxter, 2020). The list is highly enriched for (a) transporters, (b) genes that affect elemental accumulation in above-ground tissues, and (c) genes that affect the accumulation of Fe and Zn. Transporter genes became obvious candidates for studying plant nutrition when disruption allele collections were produced (McDowell et al., 2013). Above-ground tissues are easier to study without contamination from the soil, and such studies are, therefore, more prevalent. Finally, while Fe and Zn are important biochemical cofactors, these elements are likely enriched in the KIG list due to their considerable interest in the community where the ionomics approach was developed. This is further illustrated in the PANTHER GO-slim databases, where Fe was the only element to have its overrepresented response, homeostasis, and transport-related GO terms show up in the PANTHER GO-slim biological process and molecular function databases, which are selected subsets of terms meant to broadly summarize data. Overrepresented terms related to other KIG list elements are only found in the GO complete databases. Taken together, these factors warn against forming conclusions about the nature of all elemental accumulation genes based on this limited dataset.

Most entries on this list are derived from model organisms, suggesting that most of our knowledge about genes that affect elemental accumulation comes from these species. *A. thaliana* and *M. truncatula* account for 64% of the primary genes list, which is probably a lower bound for the influence of knowledge generated in model organisms. Several of the genes in crop plants were found due to being orthologs of genes in the model organisms (Ahmad, et al., 2016; Xu et al., 2017), and on closer inspection of the 50 papers identifying primary genes in rice, 38 cited a gene in Arabidopsis (not necessarily the direct ortholog) as a source for why the gene was investigated. The higher quality of the GO terms in Arabidopsis, when compared to other species, is another reflection of this disparity of knowledge and a significant hindrance when trying to clone genes in other organisms.



## 4.1 | Call for more submissions

While we have done our best to ensure that the current list is useful and thorough, it is possible we are still missing genes. We ask readers who know of genes that we are missing to contribute by submitting them here: [https://docs.google.com/forms/d/e/1FAIpQLSdmS\\_zeOlxTOLmq2wB45BuSQml1LMKtKnWSatmFRGR2Q1o0Ew/viewform?c=0&w=1](https://docs.google.com/forms/d/e/1FAIpQLSdmS_zeOlxTOLmq2wB45BuSQml1LMKtKnWSatmFRGR2Q1o0Ew/viewform?c=0&w=1) or email corresponding author. KIG lists v1.0 for each of the species can be viewed in Table S1, and future updates to the list can be found at <https://docs.google.com/spreadsheets/d/1Xl21vtVJiHrIXLeOS5yTQqNLYq7BOHpmjuC-kUeJUU/edit?usp=sharing>.

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### AUTHORS CONTRIBUTIONS

Contributed genes: IB, FKR, FM, SC, EW, PK. Analyzed data: LW, GZ. Wrote paper: LW, FKR, IB. Edited paper: FKR, FM, SC, EW, PK, GZ, LW, IB.

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### REFERENCES

- Abreu, I., Saéz, Á., Castro-Rodríguez, R., Escudero, V., Rodríguez-Haas, B., Senovilla, M., Larue, C., Grolimund, D., Tejada-Jiménez, M., Imperial, J., & González-Guerrero, M. (2017). *Medicago truncatula* zinc-iron permease6 provides zinc to rhizobia-infected nodule cells. *Plant, Cell & Environment*, *40*(11), 2706–2719.
- Aggarwal, S., Kumar, A., Bhati, K. K., Kaur, G., Shukla, V., Tiwari, S., & Pandey, A. K. (2018). RNAi-mediated downregulation of inositol pentakisphosphate kinase (IPK1) in wheat grains decreases phytic acid levels and increases Fe and Zn Accumulation. *Frontiers in Plant Science*, *9*(March), 259. <https://doi.org/10.3389/fpls.2018.00259>
- Ahmad, I., Devonshire, J., Mohamed, R., Schultze, M., & Maathuis, F. J. M. (2016). Overexpression of the potassium channel TPKb in small vacuoles confers osmotic and drought tolerance to rice. *The New Phytologist*, *209*(3), 1040–1048.
- Ahmad, I., Mian, A., & Maathuis, F. J. M. (2016). Overexpression of the rice AKT1 potassium channel affects potassium nutrition and rice drought tolerance. *Journal of Experimental Botany*, *67*(9), 2689–2698. <https://doi.org/10.1093/jxb/erw103>
- Andrés-Colás, N., Sancenón, V., Rodríguez-Navarro, S., Mayo, S., Thiele, D. J., Ecker, J. R., Puig, S., & Peñarrubia, L. (2006). The arabidopsis heavy metal P-type ATPase HMA5 interacts with metallochaperones and functions in copper detoxification of roots. *The Plant Journal*, *45*(2), 225–236. <https://doi.org/10.1111/j.1365-313X.2005.02601.x>
- Arrivault, S., Senger, T., & Krämer, U. (2006). The Arabidopsis metal tolerance protein AtMTP3 maintains metal homeostasis by mediating Zn exclusion from the shoot under Fe Deficiency and Zn oversupply. *The Plant Journal*, *46*(5), 861–879. <https://doi.org/10.1111/j.1365-313X.2006.02746.x>
- Ashburner, M., Ball, C. A., Blake, J. A., Botstein, D., Butler, H., Cherry, J. M., Davis, A. P., Dolinski, K., Dwight, S. S., Eppig, J. T., Harris, M. A., Hill, D. P., Issel-Tarver, L., Kasarskis, A., Lewis, S., Matese, J. C., Richardson, J. E., Ringwald, M., Rubin, G. M., & Sherlock, G. (2000). Gene ontology: Tool for the unification of biology. The gene ontology consortium. *Nature Genetics*, *25*(1), 25–29. <https://doi.org/10.1038/75556>
- Assunção, A. G. L., Herrero, E., Lin, Y.-F., Huettel, B., Talukdar, S., Smaczniak, C., Immink, R. G. H., van Eldik, M., Fiers, M., Schat, H., & Aarts, M. G. M. (2010). Arabidopsis thaliana transcription factors bZIP19 and bZIP23 regulate the adaptation to zinc deficiency. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(22), 10296–10301. <https://doi.org/10.1073/pnas.1004788107>
- Barberon, M., Dubeaux, G., Kolb, C., Isono, E., Zelazny, E., & Vert, G. (2014). Polarization of IRON-REGULATED TRANSPORTER 1 (IRT1) to the plant-soil interface plays crucial role in metal homeostasis. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(22), 8293–8298. <https://doi.org/10.1073/pnas.1402262111>
- Barkla, B. J., & Pantoja, O. (1996). Physiology of ion transport across the tonoplast of higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, *47*(June), 159–184. <https://doi.org/10.1146/annurev.arplant.47.1.159>
- Bashir, K., Ishimaru, Y., Shimo, H., Nagasaka, S., Fujimoto, M., Takanashi, H., Tsutsumi, N., An, G., Nakanishi, H., & Nishizawa, N. K. (2011). The Rice Mitochondrial Iron Transporter Is Essential for Plant Growth. *Nature Communications*, *2*, 322.
- Baxter, I. (2020). We aren't good at picking candidate genes, and it's slowing us down. *Current Opinion in Plant Biology*, *54*(April), 57–60.
- Baxter, I., Brazelton, J. N., Danni, Y. U., Huang, Y. S., Lahner, B., Yakubova, E., Li, Y., Bergelson, J., Borevitz, J. O., Nordborg, M., & Vitek, O. (2010). A coastal cline in sodium accumulation in arabidopsis thaliana is driven by natural variation of the sodium transporter AtHKT1;1. *PLoS Genetics*, *6*(11), e1001193.
- Baxter, I., Hosmani, P. S., Rus, A., Lahner, B., Borevitz, J. O., Muthukumar, B., Mickelbart, M. V., Schreiber, L., Franke, R. B., & Salt, D. E. (2009). Root suberin forms an extracellular barrier that affects water relations and mineral nutrition in arabidopsis. *PLoS Genetics*, *5*(5), e1000492.
- Baxter, I., Muthukumar, B., Park, H. C., Buchner, P., Lahner, B., Danku, J., Zhao, K., Lee, J., Hawkesford, M. J., Guerinot, M. L., & Salt, D. E. (2008). Variation in molybdenum content across broadly distributed populations of arabidopsis thaliana is controlled by a Mitochondrial Molybdenum Transporter (MOT1). *PLoS Genetics*, *4*(2), e1000004.
- Baxter, I. R., Vitek, O., Lahner, B., Muthukumar, B., Borghi, M., Morrissey, J., Guerinot, M. L., & Salt, D. E. (2008). The leaf ionome as a multivariable system to detect a plant's physiological status. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(33), 12081–12086.
- Bernal, M., Casero, D., Singh, V., Wilson, G. T., Grande, A., Yang, H., Dodani, S. C., Pellegrini, M., Huijser, P., Connolly, E. L., & Merchant, S. S. (2012). Transcriptome sequencing identifies SPL7-regulated copper acquisition genes FRO4/FRO5 and the copper dependence of iron homeostasis in arabidopsis. *The Plant Cell*, *24*(2), 738–761.
- Bhati, K. K., Alok, A., Kumar, A., Kaur, J., Tiwari, S., & Pandey, A. K. (2016). Silencing of ABCC13 transporter in wheat reveals its involvement in grain development, phytic acid accumulation and lateral root formation. *Journal of Experimental Botany*, *67*(14), 4379–4389.
- Borghi, M., Rus, A., & Salt, D. E. (2011). Loss-of-Function of constitutive expresser of pathogenesis related genes5 affects potassium homeostasis in arabidopsis thaliana. *PLoS One*, *6*(10), e26360.



- Cailliatte, R., Schikora, A., Briat, J.-F., Mari, S., & Curie, C. (2010). High-affinity manganese uptake by the metal transporter NRAMP1 is essential for arabidopsis growth in low manganese conditions. *The Plant Cell*, 22(3), 904–917.
- Cao, M.-J., Wang, Z., Wirtz, M., Hell, R., Oliver, D. J., & Xiang, C.-B. (2013). SULTR3;1 is a chloroplast-localized sulfate transporter in arabidopsis thaliana. *The Plant Journal*, 73(4), 607–616.
- Carbon, S., Ireland, A., Mungall, C. J., Shu, S., Marshall, B., Lewis, S., AmiGO Hub and Web Presence Working Group. (2009). AmiGO: online access to ontology and annotation data. *Bioinformatics*, 25(2), 288–289.
- Catarecha, P., Segura, M. D., Franco-Zorrilla, J. M., García-Ponce, B., Lanza, M., Solano, R., Paz-Ares, J., & Leyva, A. (2007). A mutant of the arabidopsis phosphate transporter PHT1;1 displays enhanced arsenic accumulation. *The Plant Cell*, 19(3), 1123–1133.
- Chan-Rodriguez, D., & Walker, E. L. (2018). Analysis of yellow striped mutants of zea mays reveals novel loci contributing to iron deficiency chlorosis. *Frontiers in Plant Science*, 9(February), 157.
- Chao, D.-Y., Baraniecka, P., Danku, J., Koprivova, A., Lahner, B., Luo, H., Yakubova, E., Dilkes, B., Kopriva, S., & Salt, D. E. (2014). Variation in sulfur and selenium accumulation is controlled by naturally occurring isoforms of the key sulfur assimilation enzyme ADENOSINE 5'-PHOSPHOSULFATE REDUCTASE2 across the arabidopsis species range. *Plant Physiology*, 166(3), 1593–1608.
- Chao, D.-Y., Chen, Y. I., Chen, J., Shi, S., Chen, Z., Wang, C., Danku, J. M., Zhao, F.-J., & Salt, D. E. (2014). Genome-wide association mapping identifies a new arsenate reductase enzyme critical for limiting arsenic accumulation in plants. *PLoS Biology*, 12(12), e1002009.
- Chao, D.-Y., Gable, K., Chen, M., Baxter, I., Dietrich, C. R., Cahoon, E. B., Gueriot, M. L., Lahner, B., Lü, S., Markham, J. E., & Morrissey, J. (2011). Sphingolipids in the root play an important role in regulating the leaf ionome in arabidopsis thaliana. *The Plant Cell*, 23(3), 1061–1081.
- Chao, D.-Y., Silva, A., Ivan Baxter, Y. S., Huang, M. N., Danku, J., Lahner, B., Yakubova, E., & Salt, D. E. (2012). Genome-wide association studies identify heavy metal ATPase3 as the primary determinant of natural variation in leaf cadmium in arabidopsis thaliana. *PLoS Genetics*, 8(9), e1002923.
- Che, J., Yokosho, K., Yamaji, N., & Ma, J. F. (2019). A Vacuolar phytosiderophore transporter alters iron and zinc accumulation in polished rice grains. *Plant Physiology*, 181(1), 276–288.
- Chen, J., Liu, Y. U., Ni, J., Wang, Y., Bai, Y., Shi, J., Gan, J., Zhongchang, W. U., & Ping, W. U. (2011). OsPHF1 regulates the plasma membrane localization of low- and high-affinity inorganic phosphate transporters and determines inorganic phosphate uptake and translocation in rice. *Plant Physiology*, 157(1), 269–278.
- Chen, Y. I., Sun, S.-K., Tang, Z., Liu, G., Moore, K. L., Maathuis, F. J. M., Miller, A. J., McGrath, S. P., & Zhao, F.-J. (2017). The nodulin 26-like intrinsic membrane protein OsNIP3;2 is involved in arsenite uptake by lateral roots in rice. *Journal of Experimental Botany*, 68(11), 3007–3016.
- Chen, Z., Fujii, Y., Yamaji, N., Masuda, S., Takemoto, Y., Kamiya, T., Yusuyin, Y., Iwasaki, K., Kato, S. I., Maeshima, M., & Ma, J. F. (2013). Mn tolerance in rice is mediated by MTP8.1, a member of the cation diffusion facilitator family. *Journal of Experimental Botany*, 64(14), 4375–4387.
- Chen, Z. C., Yamaji, N., Horie, T., Che, J., Li, J., An, G., & Ma, J. F. (2017). A magnesium transporter OsMGT1 plays a critical role in salt tolerance in rice. *Plant Physiology*, 174(3), 1837–1849.
- Connorton, J. M., Webster, R. E., Cheng, N., & Pittman, J. K. (2012). Knockout of multiple arabidopsis cation/H(+) exchangers suggests isoform-specific roles in metal stress response, germination and seed mineral nutrition. *PLoS One*, 7(10), e47455.
- Delhaize, E. (1996). A metal-accumulator mutant of arabidopsis thaliana. *Plant Physiology*, 111(3), 849–855.
- Deng, F., Yamaji, N., Xia, J., & Ma, J. F. (2013). A Member of the heavy metal P-Type ATPase OsHMA5 is involved in xylem loading of copper in rice. *Plant Physiology*, 163(3), 1353–1362.
- Desbrosses-Fonrouge, A.-G., Voigt, K., Schröder, A., Arrivault, S., Thomine, S., & Krämer, U. (2005). Arabidopsis thaliana MTP1 Is a Zn transporter in the vacuolar membrane which mediates Zn detoxification and drives leaf Zn accumulation. *FEBS Letters*, 579(19), 4165–4174.
- Devaiah, B. N., Madhuvanthi, R., Karthikeyan, A. S., & Raghothama, K. G. (2009). Phosphate Starvation responses and gibberellic acid biosynthesis are regulated by the MYB62 transcription factor in arabidopsis. *Molecular Plant*, 2(1), 43–58.
- Dhankher, O. P., Rosen, B. P., McKinney, E. C., & Meagher, R. B. (2006). Hyperaccumulation of Arsenic in the Shoots of Arabidopsis Silenced for Arsenate Reductase (ACR2). *Proceedings of the National Academy of Sciences of the United States of America*, 103(14), 5413–5418.
- Durbak, A. R., Phillips, K. A., Pike, S., O'Neill, M. A., Mares, J., Gallavotti, A., Malcomber, S. T., Gassmann, W., & McSteen, P. (2014). Transport of boron by the tassel-less1 aquaporin is critical for vegetative and reproductive development in maize. *The Plant Cell*, 26(7), 2978–2995.
- Eide, D., Broderius, M., Fett, J., & Gueriot, M. L. (1996). A novel iron-regulated metal transporter from plants identified by functional expression in yeast. *Proceedings of the National Academy of Sciences of the United States of America*, 93(11):5624–5628.
- Eroglu, S., Giehl, R. F. H., Meier, B., Takahashi, M., Terada, Y., Ignatyev, K., Andresen, E., Küpper, H., Peiter, E., & von Wirén, N. (2017). Metal tolerance protein 8 mediates manganese homeostasis and iron reallocation during seed development and germination. *Plant Physiology*, 174(3), 1633–1647.
- Eroglu, S., Meier, B., von Wirén, N., & Peiter, E. (2016). The vacuolar manganese transporter MTP8 determines tolerance to iron deficiency-induced chlorosis in arabidopsis. *Plant Physiology*, 170(2), 1030–1045.
- Gao, Y.-Q., Chen, J.-G., Chen, Z.-R., An, D., Lv, Q.-Y., Han, M.-L., Wang, Y.-L., Salt, D. E., & Chao, D.-Y. (2017). A new vesicle trafficking regulator CTL1 plays a crucial role in ion homeostasis. *PLoS Biology*, 15(12), e2002978.
- Gil-Díez, P., Tejada-Jiménez, M., León-Mediavilla, J., Wen, J., Mysore, K. S., Imperial, J., & González-Guerrero, M. (2018). MtMOT1.2 is responsible for molybdate supply to medicago truncatula nodules. *Plant, Cell & Environment*, 42(1), 310–320. <https://doi.org/10.1111/pce.13388>
- Gobert, A., Park, G., Amtmann, A., Sanders, D., & Maathuis, F. J. M. (2006). Arabidopsis thaliana cyclic nucleotide gated channel 3 forms a non-selective ion transporter involved in germination and cation transport. *Journal of Experimental Botany*, 57(4), 791–800.
- Guo, J., Dai, X., Wenzhong, X. U., & Ma, M. I. (2008). Overexpressing GSH1 and AsPCS1 simultaneously increases the tolerance and accumulation of cadmium and arsenic in arabidopsis thaliana. *Chemosphere*, 72(7), 1020–1026.
- Guo, K. M., Babourina, O., Christopher, D. A., Borsic, T., & Rengel, Z. (2010). The cyclic nucleotide-gated channel AtCNGC10 transports Ca<sup>2+</sup> and Mg<sup>2+</sup> in arabidopsis. *Physiologia Plantarum*, 139(3), 303–312.
- Harris, M. A., Clark, J., Ireland, A., Lomax, J., Ashburner, M., Foulger, R., Eilbeck, K. et al (2004). The gene ontology (GO) database and informatics resource. *Nucleic Acids Research*, 32(Database issue): D258–D261.
- Hayashi, S., Kuramata, M., Abe, T., Takagi, H., Ozawa, K., & Ishikawa, S. (2017). Phytochelatin synthase OsPCS1 plays a crucial role in reducing arsenic levels in rice grains. *The Plant Journal*, 91(5), 840–848.
- Haydon, M. J., Kawachi, M., Wirtz, M., Hillmer, S., Hell, R., & Krämer, U. (2012). Vacuolar nicotianamine has critical and distinct roles under iron deficiency and for zinc sequestration in arabidopsis. *The Plant Cell*, 24(2), 724–737.
- Hindt, M. N., Akmakjian, G. Z., Pivarski, K. L., Punshon, T., Baxter, I., Salt, D. E., & Gueriot, M. L. (2017). BRUTUS and Its paralogs, BTS LIKE1 and BTS LIKE2, encode important negative regulators of the



- iron deficiency response in *arabidopsis thaliana*. *Metallomics*, 9(7), 876–890.
- Hoewyk, V., Douglas, G. F., Garifullina, A. R., Ackley, S. E., Abdel-Ghany, M. A., Marcus, S. F., Ishiyama, K., Inoue, E., Pilon, M., Takahashi, H., & Pilon-Smits, E. A. (2005). Overexpression of AtCpNifS enhances selenium tolerance and accumulation in *arabidopsis*. *Plant Physiology*, 139(3), 1518–1528.
- Horie, T., Costa, A., Kim, T. H., Han, M. J., Horie, R., Leung, H.-Y., Miyao, A., Hirochika, H., An, G., & Schroeder, J. I. (2007). Rice OsHKT2;1 transporter mediates large Na<sup>+</sup> influx component into K<sup>+</sup>-starved roots for growth. *The EMBO Journal*, 26(12), 3003–3014.
- Huang, X.-Y., Chao, D.-Y., Koprivova, A., Danku, J., Wirtz, M., Müller, S., Sandoval, F. J., Bauwe, H., Roje, S., Dilkes, B., & Hell, R. (2016). Nuclear localised MORE SULPHUR ACCUMULATION1 epigenetically regulates sulphur homeostasis in *arabidopsis thaliana*. *PLoS Genetics*, 12(9), e1006298.
- Huang, X.-Y., Deng, F., Yamaji, N., Pinson, S. R. M., Fujii-Kashino, M., Danku, J., Douglas, A., Guerinot, M. L., Salt, D. E., & Ma, J. F. (2016). A heavy metal P-Type ATPase OsHMA4 prevents copper accumulation in rice grain. *Nature Communications*, 7(July), 12138.
- Huang, X.-Y., Liu, H., Zhu, Y.-F., Pinson, S. R. M., Lin, H.-X., Guerinot, M. L., Zhao, F.-J., & Salt, D. E. (2019). Natural variation in a molybdate transporter controls grain molybdenum concentration in rice. *The New Phytologist*, 221(4), 1983–1997.
- Hussain, D., Haydon, M. J., Wang, Y., Wong, E., Sherson, S. M., Young, J., Camakaris, J., Harper, J. F., & Cobbett, C. S. (2004). P-type ATPase heavy metal transporters with roles in essential zinc homeostasis in *arabidopsis*. *The Plant Cell*, 16(5), 1327–1339.
- Isayenkov, S. V., & Maathuis, F. J. M. (2008). The *arabidopsis thaliana* aquaglyceroporin AtNIP7;1 is a pathway for arsenite uptake. *FEBS Letters*, 582(11), 1625–1628.
- Ishimaru, Y., Bashir, K., Fujimoto, M., An, G., Itai, R. N., Tsutsumi, N., Nakanishi, H., & Nishizawa, N. K. (2009). Rice-specific mitochondrial iron-regulated gene (MIR) plays an important role in iron homeostasis. *Molecular Plant*, 2(5), 1059–1066.
- Ishimaru, Y., Masuda, H., Bashir, K., Inoue, H., Tsukamoto, T., Takahashi, M., Nakanishi, H., Aoki, N., Hirose, T., Ohsugi, R., & Nishizawa, N. K. (2010). Rice metal-nicotianamine transporter, OsYSL2, is required for the long-distance transport of iron and manganese. *The Plant Journal*, 62(3), 379–390.
- Kamiya, T., Borghi, M., Wang, P., Danku, J. M. C., Kalmbach, L., Hosmani, P. S., Naseer, S., Fujiwara, T., Geldner, N., & Salt, D. E. (2015). The MYB36 transcription factor orchestrates Casparian strip formation. *Proceedings of the National Academy of Sciences of the United States of America*, 112(33), 10533–10538. <https://doi.org/10.1073/pnas.1507691112>
- Kamiya, T., Yamagami, M., Hirai, M. Y., & Fujiwara, T. (2012). Establishment of an in planta magnesium monitoring system using CAX3 promoter-luciferase in *arabidopsis*. *Journal of Experimental Botany*, 63(1), 355–363. <https://doi.org/10.1093/jxb/err283>
- Khan, G. A., Bouraine, S., Wege, S., Li, Y., de Carbonnel, M., Berthomieu, P., Poirier, Y., & Rouached, H. (2014). Coordination between zinc and phosphate homeostasis involves the transcription factor PHR1, the phosphate exporter PHO1, and its homologue PHO1;H3 in *arabidopsis*. *Journal of Experimental Botany*, 65(3), 871–884. <https://doi.org/10.1093/jxb/ert444>
- Kim, D.-Y., Bovet, L., Maeshima, M., Martinoia, E., & Lee, Y. (2007). The ABC transporter AtPDR8 is a cadmium extrusion pump conferring heavy metal resistance: Role of AtPDR8 in cadmium resistance. *The Plant Journal*, 50(2), 207–218. <https://doi.org/10.1111/j.1365-313X.2007.03044.x>
- Kim, S. A., Punshon, T., Lanzirrotti, A., Li, L., Alonso, J. M., Ecker, J. R., Kaplan, J., & Guerinot, M. L. (2006). Localization of iron in *arabidopsis* seed requires the vacuolar membrane transporter VIT1. *Science*, 314(5803), 1295–1298. <https://doi.org/10.1126/science.1132563>
- Kim, Y.-Y., Choi, H., Segami, S., Cho, H.-T., Martinoia, E., Maeshima, M., & Lee, Y. (2009). AtHMA1 contributes to the detoxification of excess Zn(II) in *arabidopsis*. *The Plant Journal*, 58(5), 737–753. <https://doi.org/10.1111/j.1365-313X.2009.03818.x>
- Kisko, M., Bouain, N., Safi, A., Medici, A., Akkers, R. C., Secco, D., Fouret, G., Krouk, G., Aarts, M. G. M., Busch, W., & Rouached, H. (2018). LPCAT1 controls phosphate homeostasis in a zinc-dependent manner. *eLife*, 7, e32077. [10.7554/eLife.32077](https://doi.org/10.7554/eLife.32077)
- Klaumann, S., Nickolaus, S. D., Fürst, S. H., Starck, S., Sabine Schneider, H., Neuhaus, E., & Trentmann, O. (2011). The tonoplast copper transporter COPT5 acts as an exporter and is required for interorgan allocation of copper in *arabidopsis thaliana*. *The New Phytologist*, 192(2), 393–404. <https://doi.org/10.1111/j.1469-8137.2011.03798.x>
- Kobayashi, N. I., Yamaji, N., Yamamoto, H., Okubo, K., Ueno, H., Costa, A., Tanoi, K., Matsumura, H., Fujii-Kashino, M., Horiuchi, T., & Nayef, M. A. (2017). OsHKT1;5 mediates Na<sup>+</sup> exclusion in the vasculature to protect leaf blades and reproductive tissues from salt toxicity in rice. *The Plant Journal*, 91(4), 657–670.
- Kobayashi, T., Nagasaka, S., Senoura, T., Itai, R. N., Nakanishi, H., & Nishizawa, N. K. (2013). Iron-binding haemerythrin RING ubiquitin ligases regulate plant iron responses and accumulation. *Nature Communications*, 4, 2792. <https://doi.org/10.1038/ncomms3792>
- Koprivova, A., Giovannetti, M., Baraniecka, P., Lee, B.-R., Grondin, C., Loudet, O., & Kopriva, S. (2013). Natural variation in the ATP5S isoform of ATP sulfurylase contributes to the control of sulfate levels in *arabidopsis*. *Plant Physiology*, 163(3), 1133–1141.
- Kühnlenz, T., Hofmann, C., Uruguchi, S., Schmidt, H., Schempp, S., Weber, M., Lahner, B., Salt, D. E., & Clemens, S. (2016). Phytochelatin synthesis promotes leaf Zn accumulation of *arabidopsis thaliana* plants grown in soil with adequate Zn supply and is essential for survival on Zn-contaminated soil. *Plant & Cell Physiology*, 57(11), 2342–2352.
- Lagarde, D., Basset, M., Lepetit, M., Conejero, G., Gaymard, F., Astruc, S., & Grignon, C. (1996). Tissue-specific expression of *arabidopsis* AKT1 gene is consistent with a role in K<sup>+</sup> nutrition. *The Plant Journal*, 9(2), 195–203.
- Lanquar, V., Ramos, M. S., Lelièvre, F., Barbier-Brygoo, H., Krieger-Liszka, A., Krämer, U., & Thomine, S. (2010). Export of vacuolar manganese by AtNRAMP3 and AtNRAMP4 is required for optimal photosynthesis and growth under manganese deficiency. *Plant Physiology*, 152(4), 1986–1999.
- Laurie, S., Feeney, K. A., Maathuis, F. J. M., Heard, P. J., Brown, S. J., & Leigh, R. A. (2002). A role for HKT1 in sodium uptake by wheat roots. *The Plant Journal*, 32(2), 139–149.
- Lee, S., Chiecko, J. C., Kim, S. A., Walker, E. L., Lee, Y., Guerinot, M. L., & An, G. (2009). Disruption of OsYSL15 leads to iron inefficiency in rice plants. *Plant Physiology*, 150(2), 786–800.
- Lee, S., Jeong, H. J., Kim, S. A., Lee, J., Guerinot, M. L., & An, G. (2010). OsZIP5 is a plasma membrane zinc transporter in rice. *Plant Molecular Biology*, 73(4–5), 507–517.
- Lee, S., Kim, Y.-S., Jeon, U. S., Kim, Y.-K., Schjoerring, J. K., & An, G. (2012). Activation of rice nicotianamine synthase 2 (OsNAS2) enhances iron availability for biofortification. *Molecules and Cells*, 33(3), 269–275.
- León-Mediavilla, J., Senovilla, M., Montiel, J., Gil-Díez, P., Saez, Á., Kryvoruchko, I. S., Reguera, M., Udvardi, M. K., Imperial, J., & González-Guerrero, M. (2018). MtMTP2-facilitated zinc transport into intracellular compartments is essential for nodule development in medicago truncatula. *Frontiers in Plant Science*, 9(July), 990.
- Li, H., Miao, Y. U., Xin-Qiao, D. U., Wang, Z.-F., Wei-Hua, W. U., Quintero, F. J., Jin, X.-H., Li, H.-D., & Wang, Y. I. (2017). NRT1.5/NPF7.3 functions as a proton-coupled H<sup>+</sup>/K<sup>+</sup> antiporter for K<sup>+</sup> loading into the xylem in *arabidopsis*. *The Plant Cell*, 29(8), 2016–2026.
- Li, X., Zhang, H., Ai, Q., Liang, G., & Diqui, Y. U. (2016). Two bHLH transcription factors, bHLH34 and bHLH104, regulate iron homeostasis in *arabidopsis thaliana*. *Plant Physiology*, 170(4), 2478–2493.
- Lin, Y.-F., Liang, H.-M., Yang, S.-Y., Boch, A., Clemens, S., Chen, C.-C., Jing-Fen, W. U., Huang, J.-L., & Yeh, K.-C. (2009). *Arabidopsis* IRT3



- Is a zinc-regulated and plasma membrane localized zinc/iron transporter. *The New Phytologist*, 182(2), 392–404.
- Lindsay, E. R., & Maathuis, F. J. M. (2016). Arabidopsis thaliana NIP7;1 is involved in tissue arsenic distribution and tolerance in response to arsenate. *FEBS Letters*, 590(6), 779–786.
- Liu, T.-Y., Huang, T.-K., Tseng, C.-Y., Lai, Y.-S., Lin, S.-I., Lin, W.-Y., Chen, J.-W., & Chiou, T.-J. (2012). PHO2-dependent degradation of PHO1 modulates phosphate homeostasis in arabidopsis. *The Plant Cell*, 24(5), 2168–2183.
- Liu, X.-M., An, J., Han, H. J., Kim, S. H., Lim, C. O., Yun, D.-J., & Chung, W. S. (2014). ZAT11, a zinc finger transcription factor, is a negative regulator of nickel ion tolerance in arabidopsis. *Plant Cell Reports*, 33(12), 2015–2021.
- Long, T. A., Tsukagoshi, H., Busch, W., Lahner, B., Salt, D. E., & Benfey, P. N. (2010). The bHLH transcription factor POPEYE regulates response to iron deficiency in arabidopsis roots. *The Plant Cell*, 22(7), 2219–2236.
- Loudet, O., Saliba-Colombani, V., Camilleri, C., Calenge, F., Gaudon, V., Koprivova, A., North, K. A., Kopriva, S., & Daniel-Vedele, F. (2007). Natural variation for sulfate content in arabidopsis thaliana is highly controlled by APR2. *Nature Genetics*, 39(7), 896–900.
- Mao, D., Chen, J., Tian, L., Liu, Z., Yang, L., Tang, R., Li, J., Lu, C., Yang, Y., Shi, J., & Chen, L. (2014). Arabidopsis transporter MGT6 mediates magnesium uptake and is required for growth under magnesium limitation. *The Plant Cell*, 26(5), 2234–2248.
- McDowell, S. C., Akmakjian, G., Sladek, C., Mendoza-Cozatl, D., Morrissey, J. B., Saini, N., Mittler, R., Baxter, I., Salt, D. E., Ward, J. M., & Schroeder, J. I. (2013). Elemental concentrations in the seed of mutants and natural variants of arabidopsis thaliana grown under varying soil conditions. *PLoS One*, 8(5), e63014.
- Mi, H., Huang, X., Muruganujan, A., Tang, H., Mills, C., Kang, D., & Thomas, P. D. (2017). PANTHER version 11: Expanded annotation data from gene ontology and reactome pathways, and data analysis tool enhancements. *Nucleic Acids Research*, 45(D1), D183–D189.
- Milner, M. J., Seamon, J., Craft, E., & Kochian, L. V. (2013). Transport properties of members of the ZIP family in plants and their role in Zn and Mn homeostasis. *Journal of Experimental Botany*, 64(1), 369–381.
- Miwa, K., Takano, J., & Fujiwara, T. (2006). Improvement of seed yields under boron-limiting conditions through overexpression of BOR1, a boron transporter for xylem loading, in arabidopsis thaliana. *The Plant Journal*, 46(6), 1084–1091.
- Miwa, K., Wakuta, S., Takada, S., Ide, K., Takano, J., Naito, S., Omori, H., Matsunaga, T., & Fujiwara, T. (2013). Roles of BOR2, a boron exporter, in cross linking of rhamnogalacturonan II and root elongation under boron limitation in arabidopsis. *Plant Physiology*, 163(4), 1699–1709.
- Morrissey, J., Baxter, I. R., Lee, J., Li, L., Lahner, B., Grotz, N., Kaplan, J., Salt, D. E., & Gueriot, M. L. (2009). The ferroportin metal efflux proteins function in iron and cobalt homeostasis in arabidopsis. *The Plant Cell*, 21(10), 3326–3338.
- Nagarajan, V. K., Jain, A., Poling, M. D., Lewis, A. J., Raghothama, K. G., & Smith, A. P. (2011). Arabidopsis Pht1;5 mobilizes phosphate between source and sink organs and influences the interaction between phosphate homeostasis and ethylene signaling. *Plant Physiology*, 156(3), 1149–1163.
- Nakagawa, Y., Hanaoka, H., Kobayashi, M., Miyoshi, K., Miwa, K., & Fujiwara, T. (2007). Cell-type specificity of the expression of Os BOR1, a rice efflux boron transporter gene, is regulated in response to boron availability for efficient boron uptake and xylem loading. *The Plant Cell*, 19(8), 2624–2635.
- Nilsson, L., Müller, R., & Nielsen, T. H. (2007). Increased expression of the MYB-related transcription factor, PHR1, leads to enhanced phosphate uptake in arabidopsis thaliana. *Plant, Cell & Environment*, 30(12), 1499–1512.
- Olsen, L. I., Hansen, T. H., Larue, C., Østerberg, J. T., Hoffmann, R. D., Liesche, J., Krämer, U., Surblé, S., Cadarsi, S., Samson, V. A., & Grolimund, D. (2016). Mother-plant-mediated pumping of zinc into the developing seed. *Nature Plants*, 2(5), 16036.
- Palmer, C. M., Hindt, M. N., Schmidt, H., Clemens, S., & Gueriot, M. L. (2013). MYB10 and MYB72 are required for growth under iron-limiting conditions. *PLoS Genetics*, 9(11), e1003953.
- Park, J., Song, W.-Y., Ko, D., Eom, Y., Hansen, T. H., Schiller, M., Lee, T. G., Martinoia, E., & Lee, Y. (2012). The phytochelatin transporters AtABCC1 and AtABCC2 mediate tolerance to cadmium and mercury: ABC transporters for PC-dependent Cd and Hg tolerance. *The Plant Journal*, 69(2), 278–288.
- Peiter, E., Montanini, B., Gobert, A., Pedas, P., Husted, S., Maathuis, F. J. M., Blaudez, D., Chalot, M., & Sanders, D. (2007). A secretory pathway-localized cation diffusion facilitator confers plant manganese tolerance. *Proceedings of the National Academy of Sciences of the United States of America*, 104(20), 8532–8537.
- Pita-Barbosa, A., Ricachenevsky, F. K., Wilson, M., Dottorini, T., & Salt, D. E. (2019). Transcriptional plasticity buffers genetic variation in zinc homeostasis. *Scientific Reports*, 9(1), 19482.
- Pottier, M., Dumont, J., Masclaux-Daubresse, C., & Thomine, S. (2019). Autophagy is essential for optimal translocation of iron to seeds in arabidopsis. *Journal of Experimental Botany*, 70(3), 859–869.
- Qi, Z., Hampton, C. R., Shin, R., Barkla, B. J., White, P. J., & Schachtman, D. P. (2008). The HIGH Affinity K<sup>+</sup> transporter AtHAK5 plays a physiological role in planta at very low K<sup>+</sup> concentrations and provides a caesium uptake pathway in arabidopsis. *Journal of Experimental Botany*, 59(3), 595–607.
- Qin, Y.-J., Wei-Hua, W. U., & Wang, Y. I. (2019). ZmHAK5 and ZmHAK1 function in K<sup>+</sup> uptake and distribution in maize under low K<sup>+</sup> conditions. *Journal of Integrative Plant Biology*, 61(6), 691–705.
- Rai, H., Yokoyama, S., Satoh-Nagasawa, N., Furukawa, J., Nomi, T., Ito, Y., Fujimura, S., Takahashi, H., Suzuki, R., Yousra, E., & Goto, A. (2017). Cesium uptake by rice roots largely depends upon a single gene, HAK1, which encodes a potassium transporter. *Plant & Cell Physiology*, 58(9), 1486–1493.
- Rampey, R. A., Woodward, A. W., Hobbs, B. N., Tierney, M. P., Lahner, B., Salt, D. E., & Bartel, B. (2006). An arabidopsis basic helix-loop-helix leucine zipper protein modulates metal homeostasis and auxin conjugate responsiveness. *Genetics*, 174(4), 1841–1857.
- Remm, M., Storm, C. E., & Sonnhammer, E. L. (2001). Automatic clustering of orthologs and in-paralogs from pairwise species comparisons. *Journal of Molecular Biology*, 314(5), 1041–1052.
- Remy, E., Cabrito, T. R., Batista, R. A., Teixeira, M. C., Sá-Correia, I., & Duque, P. (2012). The Pht1;9 and Pht1;8 transporters mediate inorganic phosphate acquisition by the arabidopsis thaliana root during phosphorus starvation. *The New Phytologist*, 195(2), 356–371.
- Remy, E., Cabrito, T. R., Batista, R. A., Teixeira, M. C., Sá-Correia, I., & Duque, P. (2015). The major facilitator superfamily transporter ZIFL2 modulates cesium and potassium homeostasis in arabidopsis. *Plant & Cell Physiology*, 56(1), 148–162.
- Ren, X.-L., Qi, G.-N., Feng, H.-Q., Zhao, S., Zhao, S.-S., Wang, Y. I., & Wei-Hua, W. U. (2013). Calcineurin B-like protein CBL10 directly interacts with AKT1 and modulates K<sup>+</sup> homeostasis in arabidopsis. *The Plant Journal*, 74(2), 258–266.
- Ren, Y., Liu, Y., Chen, H., Li, G., Zhang, X., & Zhao, J. (2012). Type 4 metallothionein genes are involved in regulating Zn ion accumulation in late embryo and in controlling early seedling growth in arabidopsis. *Plant, Cell & Environment*, 35(4), 770–789. <https://doi.org/10.1111/j.1365-3040.2011.02450.x>
- Ren, Z.-H., Gao, J.-P., Li, L.-G., Cai, X.-L., Huang, W., Chao, D.-Y., Zhu, M.-Z., Wang, Z.-Y., Luan, S., & Lin, H.-X. (2005). A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nature Genetics*, 37(10), 1141–1146. <https://doi.org/10.1038/ng1643>
- Robinson, N. J., Procter, C. M., Connolly, E. L., & Gueriot, M. L. (1999). A ferric-chelate reductase for iron uptake from soils. *Nature*, 397(February), 694. <https://doi.org/10.1038/17800>



- Rubio, F., Nieves-Cordones, M., Alemán, F., & Martínez, V. (2008). Relative contribution of AtHAK5 and AtAKT1 to K<sup>+</sup> uptake in the high-affinity range of concentrations. *Physiologia Plantarum*, 134(4), 598–608.
- Sancenón, V., Puig, S., Mateu-Andrés, I., Dorcey, E., Thiele, D. J., & Peñarrubia, L. (2004). The arabidopsis copper transporter COPT1 functions in root elongation and pollen development. *The Journal of Biological Chemistry*, 279(15), 15348–15355.
- Sanjaya, P.-Y., Ruey-Chih, S. U., Ko, S.-S., Tong, C.-G., Yang, R.-Y., & Chan, M.-T. (2008). Overexpression of arabidopsis thaliana tryptophan synthase beta 1 (AtTSB1) in arabidopsis and tomato confers tolerance to cadmium stress. *Plant, Cell & Environment*, 31(8), 1074–1085.
- Sasaki, A., Yamaji, N., Mitani-Ueno, N., Kashino, M., & Ma, J. F. (2015). A node-localized transporter OsZIP3 is responsible for the preferential distribution of Zn to developing tissues in rice. *The Plant Journal*, 84(2), 374–384. <https://doi.org/10.1111/tpj.13005>
- Sasaki, A., Yamaji, N., Yokosho, K., & Ma, J. F. (2012). Nramp5 is a major transporter responsible for manganese and cadmium uptake in rice. *The Plant Cell*, 24(5), 2155–2167. <https://doi.org/10.1105/tpc.112.096925>
- Schaaf, G., Honsbein, A., Meda, A. R., Kirchner, S., Wipf, D., & von Wirén, N. (2006). AtIREG2 encodes a tonoplast transport protein involved in iron-dependent nickel detoxification in arabidopsis thaliana roots. *The Journal of Biological Chemistry*, 281(35), 25532–25540.
- Secco, D., Baumann, A., & Poirier, Y. (2010). Characterization of the rice PHO1 gene family reveals a key role for ospho1;2 in phosphate homeostasis and the evolution of a distinct clade in dicotyledons. *Plant Physiology*, 152(3), 1693–1704.
- Selote, D., Samira, R., Matthiadis, A., Gillikin, J. W., & Long, T. A. (2015). Iron-binding E3 ligase mediates iron response in plants by targeting basic helix-loop-helix transcription factors. *Plant Physiology*, 167(1), 273–286.
- Senoura, T., Sakashita, E., Kobayashi, T., Takahashi, M., Aung, M. S., Masuda, H., Nakanishi, H., & Nishizawa, N. K. (2017). The iron-chelate transporter OsYSL9 plays a role in iron distribution in developing rice grains. *Plant Molecular Biology*, 95(4–5), 375–387.
- Senovilla, M., Castro-Rodríguez, R., Abreu, I., Escudero, V., Kryvoruchko, I., Udvardi, M. K., Imperial, J., & González-Guerrero, M. (2018). Medicago truncatula copper transporter 1 (MtCOPT1) delivers copper for symbiotic nitrogen fixation. *The New Phytologist*, 218(2), 696–709.
- Shi, H., Lee, B.-H., Shaw-Jye, W. U., & Zhu, J.-K. (2003). Overexpression of a plasma membrane Na<sup>+</sup>/H<sup>+</sup> antiporter gene improves salt tolerance in arabidopsis thaliana. *Nature Biotechnology*, 21(1), 81–85.
- Shin, H., Shin, H.-S., Dewbre, G. R., & Harrison, M. J. (2004). Phosphate transport in arabidopsis: Pht1;1 and Pht1;4 play a major role in phosphate acquisition from both low- and high-phosphate environments. *The Plant Journal*, 39(4), 629–642.
- Shin, L.-J., Lo, J.-C., & Yeh, K.-C. (2012). Copper chaperone antioxidant protein1 is essential for copper homeostasis. *Plant Physiology*, 159(3), 1099–1110.
- Song, W.-Y., Choi, K. S., Kim, D. Y., Geisler, M., Park, J., Vincenzetti, V., Schellenberg, M., Kim, S. H., Lim, Y. P., Noh, E. W., Lee, Y., & Martinoia, E. (2010). Arabidopsis PCR2 is a zinc exporter involved in both zinc extrusion and long-distance zinc transport. *The Plant Cell*, 22(7), 2237–2252.
- Song, W.-Y., Yamaki, T., Yamaji, N., Ko, D., Jung, K.-H., Fujii-Kashino, M., An, G., Martinoia, E., Lee, Y., & Ma, J. F. (2014). A Rice ABC transporter, OsABCC1, reduces arsenic accumulation in the grain. *Proceedings of the National Academy of Sciences of the United States of America*, 111(44), 15699–15704.
- Stoeger, T., Gerlach, M., Morimoto, R. I., & Nunes, L. A. (2018). Large-scale investigation of the reasons why potentially important genes are ignored. *PLoS Biology*, 16(9), e2006643.
- Sun, S.-K., Chen, Y. I., Che, J., Konishi, N., Tang, Z., Miller, A. J., Ma, J. F., & Zhao, F.-J. (2018). Decreasing arsenic accumulation in rice by overexpressing OsNIP1;1 and OsNIP3;3 through disrupting arsenite radial transport in roots. *The New Phytologist*, 219(2), 641–653.
- Sunkar, R., Kaplan, B., Bouché, N., Arazi, T., Dolev, D., Talke, I. N., Maathuis, F. J., Sanders, D., Bouchez, D., & Fromm, H. (2000). Expression of a truncated tobacco NtCBP4 channel in transgenic plants and disruption of the homologous arabidopsis CNGC1 gene confer Pb<sup>2+</sup> tolerance. *The Plant Journal*, 24(4), 533–542.
- Takahashi, R., Ishimaru, Y., Shimo, H., Ogo, Y., Senoura, T., Nishizawa, N. K., & Nakanishi, H. (2012). The OsHMA2 transporter is involved in root-to-shoot translocation of Zn and Cd in rice. *Plant, Cell & Environment*, 35(11), 1948–1957.
- Takano, J., Wada, M., Ludewig, U., Schaaf, G., von Wirén, N., & Fujiwara, T. (2006). The arabidopsis major intrinsic protein NIP5;1 is essential for efficient boron uptake and plant development under boron limitation. *The Plant Cell*, 18(6), 1498–1509.
- Takemoto, Y., Tsunemitsu, Y., Fujii-Kashino, M., Mitani-Ueno, N., Yamaji, N., Ma, J. F., Kato, S.-I., Iwasaki, K., & Ueno, D. (2017). The tonoplast-localized transporter MTP8.2 contributes to manganese detoxification in the shoots and roots of *Oryza Sativa* L. *Plant & Cell Physiology*, 58(9), 1573–1582.
- Tanaka, M., Wallace, I. S., Takano, J., Roberts, D. M., & Fujiwara, T. (2008). NIP6;1 is a boric acid channel for preferential transport of boron to growing shoot tissues in arabidopsis. *The Plant Cell*, 20(10), 2860–2875.
- Tanaka, N., Nishida, S., Kamiya, T., & Fujiwara, T. (2016). Large-scale profiling of brown rice ionome in an ethyl methanesulphonate-mutagenized hitomebore population and identification of high- and low-cadmium lines. *Plant and Soil*, 407(1–2), 109–117.
- Tarantino, D., Morandini, P., Ramirez, L., Soave, C., & Murgia, I. (2011). Identification of an arabidopsis mitoferrinlike carrier protein involved in Fe metabolism. *Plant Physiology and Biochemistry*, 49(5), 520–529.
- Tejada-Jiménez, M., Castro-Rodríguez, R., Igor Kryvoruchko, M., Lucas, M., Udvardi, M., Imperial, J., & González-Guerrero, M. (2015). Medicago truncatula natural resistance-associated macrophage protein1 is required for iron uptake by rhizobia-infected nodule cells. *Plant Physiology*, 168(1), 258–272.
- Tejada-Jiménez, M., Gil-Díez, P., León-Mediavilla, J., Wen, J., Mysore, K. S., Imperial, J., & González-Guerrero, M. (2017). Medicago truncatula Molybdate Transporter Type 1 (MtMOT1.3) is a plasma membrane molybdenum transporter required for nitrogenase activity in root nodules under molybdenum deficiency. *The New Phytologist*, 216(4), 1223–1235.
- The Gene Ontology Consortium (2017). Expansion of the gene ontology knowledgebase and resources. *Nucleic Acids Research*, 45(D1), D331–D338.
- Tian, H., Baxter, I. R., Lahner, B., Reinders, A., Salt, D. E., & Ward, J. M. (2010). Arabidopsis NPCC6/NaKR1 is a phloem mobile metal binding protein necessary for phloem function and root meristem maintenance. *The Plant Cell*, 22(12), 3963–3979.
- Ueno, D., Sasaki, A., Yamaji, N., Miyaji, T., Fujii, Y., Takemoto, Y., Moriyama, S., Che, J., Moriyama, Y., Iwasaki, K., & Ma, J. F. (2015). A polarly localized transporter for efficient manganese uptake in rice. *Nature Plants*, 1(November), 15170.
- Uraguchi, S., Tanaka, N., Hofmann, C., Abiko, K., Ohkama-Ohtsu, N., Weber, M., Kamiya, T., Sone, Y., Nakamura, R., Takanezawa, Y., & Kiyono, M., (2017). Phytochelatin synthase has contrasting effects on cadmium and arsenic accumulation in rice grains. *Plant & Cell Physiology*, 58(10), 1730–1742.
- Vitart, V., Baxter, I., Doerner, P., & Harper, J. F. (2001). Evidence for a role in growth and salt resistance of a plasma membrane H<sup>+</sup>-ATPase in the root endodermis: salt sensitive H<sup>+</sup>-ATPase mutant. *The Plant Journal*, 27(3), 191–201.



- Von Wiren, N., Mori, S., Marschner, H., & Romheld, V. (1994). Iron inefficiency in maize mutant ys1 (*Zea Mays* L. Cv Yellow-Stripe) is caused by a defect in uptake of iron phytosiderophores. *Plant Physiology*, 106(1), 71–77.
- Wang, C., Ying, S., Huang, H., Li, K., Ping, W. U., & Shou, H. (2009). Involvement of OsSPX1 in phosphate homeostasis in rice. *The Plant Journal*, 57(5), 895–904.
- Wang, J., Sun, J., Miao, J., Guo, J., Shi, Z., He, M., Chen, Y., Zhao, X., Li, B., Han, F., & Tong, Y. (2013). A phosphate starvation response regulator Ta-Phr1 is involved in phosphate signalling and increases grain yield in wheat. *Annals of Botany*, 111(6), 1139–1153.
- Wang, L. U., Ying, Y., Narsai, R., Ye, L., Zheng, L., Tian, J., Whelan, J., & Shou, H. (2013). Identification of OsbHLH133 as a regulator of iron distribution between roots and shoots in *Oryza Sativa*. *Plant, Cell & Environment*, 36(1), 224–236.
- Waters, B. M., Chu, H.-H., Didonato, R. J., Roberts, L. A., Eisle, R. B., Lahner, B., Salt, D. E., & Walker, E. L. (2006). Mutations in arabidopsis yellow stripe-like1 and yellow stripe-like3 reveal their roles in metal ion homeostasis and loading of metal ions in seeds. *Plant Physiology*, 141(4), 1446–1458.
- Wild, M., Davière, J.-M., Regnault, T., Sakvarelidze-Achard, L., Carrera, E., Diaz, I. L., Cayrel, A., Dubeaux, G., Vert, G., & Achard, P. (2016). Tissue-specific regulation of gibberellin signaling fine-tunes arabidopsis iron-deficiency responses. *Developmental Cell*, 37(2), 190–200.
- Wimalanathan, K., Friedberg, I., Andorf, C. M., & Lawrence-Dill, C. J. (2018). Maize GO annotation—methods, evaluation, and review (maize-GAMER). *Plant Direct*, 2(4), e00052.
- Xu, J., Li, H.-D., Chen, L.-Q., Wang, Y. I., Liu, L.-L., He, L., & Wei-Hua, W. U. (2006). A protein kinase, interacting with two calcineurin B-like proteins, regulates K<sup>+</sup> transporter AKT1 in arabidopsis. *Cell*, 125(7), 1347–1360.
- Xu, J., Shi, S., Wang, L., Tang, Z., Lv, T., Zhu, X., Ding, X., Wang, Y., Zhao, F.-J., & Zhongchang, W. U. (2017). OsHAC4 is critical for arsenate tolerance and regulates arsenic accumulation in rice. *The New Phytologist*, 215(3), 1090–1101.
- Xu, W., Dai, W., Yan, H., Li, S., Shen, H., Chen, Y., Hua, X. U., Sun, Y., He, Z., & Ma, M. I. (2015). Arabidopsis NIP3;1 plays an important role in arsenic uptake and root-to-shoot translocation under arsenite stress conditions. *Molecular Plant*, 8(5), 722–733.
- Yamaji, N., Takemoto, Y., Miyaji, T., Mitani-Ueno, N., Yoshida, K. T., & Ma, J. F. (2017). Reducing phosphorus accumulation in rice grains with an impaired transporter in the node. *Nature*, 541(7635), 92–95.
- Yan, J., Chia, J.-C., Sheng, H., Jung, H.-I., Tetiana-Olena Zavodna, L. U., Zhang, R. H., Zavodna, T. O., Zhang, L., Huang, R., Jiao, C., Craft, E. J., Fei, Z., & Kochian, L. V. (2017). Arabidopsis pollen fertility requires the transcription factors CITF1 and SPL7 that regulate copper delivery to anthers and jasmonic acid synthesis. *The Plant Cell*, 29(12), 3012–3029.
- Yan, J., Wang, P., Wang, P., Yang, M., Lian, X., Tang, Z., Huang, C.-F., Salt, D. E., & Zhao, F. J. (2016). A loss-of-function allele of OsHMA3 associated with high cadmium accumulation in shoots and grain of japonica rice cultivars. *Plant, Cell & Environment*, 39(9), 1941–1954.
- Yang, A. N., Li, Y., Yunyuan, X. U., & Zhang, W.-H. (2013). A receptor-like protein RMC is involved in regulation of iron acquisition in rice. *Journal of Experimental Botany*, 64(16), 5009–5020.
- Yang, A. N., & Zhang, W.-H. (2016). A small GTPase, OsRab6a, is involved in the regulation of iron homeostasis in rice. *Plant & Cell Physiology*, 57(6), 1271–1280.
- Yuan, Y., Huilan, W. U., Wang, N., Li, J., Zhao, W., Juan, D. U., Wang, D., & Ling, H.-Q. (2008). FIT interacts with AtbHLH38 and AtbHLH39 in regulating iron uptake gene expression for iron homeostasis in arabidopsis. *Cell Research*, 18(3), 385–397.
- Zhai, Z., Gayomba, S. R., Jung, H.-I., Vimalakumari, N. K., Piñeros, M., Craft, E., Rutzke, M. A., Danku, J., Lahner, B., Punshon, T., & Guerinot, M. L. (2014). OPT3 is a phloem-specific iron transporter that is essential for systemic iron signaling and redistribution of iron and cadmium in arabidopsis. *The Plant Cell*, 26(5), 2249–2264.
- Zhang, H., Li, Y., Yao, X., Liang, G., & Diqiu, Y. U. (2017). POSITIVE REGULATOR OF IRON HOMEOSTASIS1, OsPR11, facilitates iron homeostasis. *Plant Physiology*, 175(1), 543–554.
- Zhang, L., Bin, H. U., Li, W., Che, R., Deng, K., Li, H., Feiyan, Y. U., Ling, H., Li, Y., & Chu, C. (2014). OsPT2, a phosphate transporter, is involved in the active uptake of selenite in rice. *The New Phytologist*, 201(4), 1183–1191.
- Zhang, M., Cao, Y., Wang, Z., Wang, Z.-Q., Shi, J., Liang, X., Song, W., Chen, Q., Lai, J., & Jiang, C. (2018). A retrotransposon in an HKT1 family sodium transporter causes variation of leaf Na<sup>+</sup> exclusion and salt tolerance in maize. *The New Phytologist*, 217(3), 1161–1176.
- Zhang, Y., Chen, K., Zhao, F.-J., Sun, C., Jin, C., Shi, Y., Sun, Y., Li, Y., Yang, M., Jing, X., & Luo, J. (2018). OsATX1 interacts with heavy metal P1B-Type ATPases and affects copper transport and distribution. *Plant Physiology*, 178(1), 329–344.
- Zhang, Y. U., Yong-Han, X. U., Yi, H.-Y., & Gong, J.-M. (2012). Vacuolar membrane transporters OsVIT1 and OsVIT2 modulate iron translocation between flag leaves and seeds in rice. *The Plant Journal: For Cell and Molecular Biology*, 72(3), 400–410.
- Zhao, M., Ding, H., Zhu, J.-K., Zhang, F., & Li, W.-X. (2011). Involvement of miR169 in the nitrogen-starvation responses in arabidopsis. *The New Phytologist*, 190(4), 906–915.
- Zhao, X. Q., Mitani, N., Yamaji, N., Shen, R. F., & Ma, J. F. (2010). Involvement of silicon influx transporter OsNIP2;1 in selenite uptake in rice. *Plant Physiology*, 153(4), 1871–1877.
- Zheng, L., Yamaji, N., Yokosho, K., & Ma, J. F. (2012). YSL16 is a phloem-localized transporter of the copper-nicotianamine complex that is responsible for copper distribution in rice. *The Plant Cell*, 24(9), 3767–3782. <https://doi.org/10.1105/tpc.112.103820>
- Zhou, J., Jiao, F., Zhongchang, W. U., Li, Y., Wang, X., He, X., Zhong, W., & Ping, W. U. (2008). OsPHR2 is involved in phosphate-starvation signaling and excessive phosphate accumulation in shoots of plants. *Plant Physiology*, 146(4), 1673–1686.
- Zhu, J., Lau, K., Puschmann, R., Harmel, R. K., Zhang, Y., Pries, V., Gaugler, P., Broger, L., Dutta, A. K., Jessen, H. J., Schaaf, G., Fernie, A. R., Hothorn, L. A., Fiedler, D., & Hothorn, M. (2019). Two bifunctional inositol pyrophosphate kinases/phosphatases control plant phosphate homeostasis. *eLife*, 8, e43582. <https://doi.org/10.7554/eLife.43582>
- Zimeri, A. M., Dhankher, O. P., McCaig, B., & Meagher, R. B. (2005). The plant MT1 metallothioneins are stabilized by binding cadmiums and are required for cadmium tolerance and accumulation. *Plant Molecular Biology*, 58(6), 839–855. <https://doi.org/10.1007/s11103-005-8268-3>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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