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A curated list of genes that control elemental accumulation in plants.

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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.

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; I. 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,

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such as *Arabidopsis thaliana* and rice (*Oryza sativa*), including Na^+ transporters from the HKT family (Z.-H. Ren et al. 2005; I. Baxter et al. 2010); the heavy metal transporters AtHMA3 and OsHMA3 (Chao et al. 2012; Jiali Yan et al. 2016); E3 ubiquitin ligase BRUTUS and OsHRZs that regulate degradation of iron uptake factors (Selote et al. 2015; Hindt et al. 2017; T. Kobayashi et al. 2013) and the K^+ channel AKT1 (Lagarde et al. 1996; Ahmad, Mian, and Maathuis 2016). 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.

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 over expressor). For double mutants, both genes are listed.
2) The levels of at least one element are significantly altered in a 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 Ionomicshub 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.

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, Storm, and Sonnhammer 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.

Gene Enrichment analysis

Overrepresentation analysis (released 07-11-2019) 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; The Gene

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Ontology Consortium 2017; Mi et al. 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 in 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 phytochelatins, other chemical reactions or pathways of metal chelator synthesis
4. Response to ions - vaguely states a 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 to 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.

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)
A.thaliana	**AT1G01340**	**CNGC10**	**K,Ca,Mg**	**Roots,shoots**	(K. M. Guo et al. 2010)
A.thaliana	**AT1G01580**	**FRO2**	**Fe**	**Root**	(Robinson et al. 1999)
A.thaliana	**AT1G07600**	**MT1A**	**Cd,Zn,As**	**Shoots**	(Zimeri et al. 2005)
A.thaliana	**AT1G08490**	**CPNIFS**	**Se,S**	**Roots,shoots**	(Van Hoewyk et al. 2005)
A.thaliana	**AT1G12640**	**LPCAT1**	**P**	**Leaf**	(Kisko et al. 2018)

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A.thaliana	**AT1G14040**	**PHO1;H3**	**P**	**Shoots**	(Khan et al. 2014)
A.thaliana	**AT1G14870**	**PCR2**	**Zn**	**Shoots**	(Song et al. 2010)
A.thaliana	**AT1G18910**	**BTSL2**	**Fe,Mn,Zn**	**Leaf**	(Hindt et al. 2017)
A.thaliana	**AT1G20110**	**FYVE1**	**Fe,Zn,Co,Mn**	**Root**	(Barberon et al. 2014)
A.thaliana	**AT1G30270**	**CIPK23**	**K**	**Shoots**	(Jiang Xu et al. 2006)
A.thaliana	**AT1G30400**	**ABCC1**	**Cd**	**Shoots**	(Park et al. 2012)
A.thaliana	**AT1G30450**	**CCC**	**Ca,K,Na,S**	**seeds**	(McDowell et al. 2013)
A.thaliana	**AT1G31885**	**NIP3;1**	**As**	**Shoots**	(W. Xu et al. 2015)
A.thaliana	**AT1G32450**	**AtNRT1.5 / AtNPF7.3**	**K, NO3-**	**Shoots, Roots**	(H. Li et al. 2017)
A.thaliana	**AT1G36370**	**AtMSA1**	**S, Se**	**Shoots**	(Huang, Chao, et al. 2016)
A.thaliana	**AT1G56160**	**myb72**	**Fe,Cd,Zn,Co,Mo**	**Leaf**	(Palmer et al. 2013)
A.thaliana	**AT1G56430**	**NAS4**	**Fe,Cd,Co,Mo**	**Leaf**	(Palmer et al. 2013)
A.thaliana	**AT1G59870**	**PEN3**	**Cd**	**Shoots, roots**	(D.-Y. Kim et al. 2007)
A.thaliana	**AT1G60960**	**AtIRT3**	**Fe**	**Roots**	(Lin et al. 2009)
A.thaliana	**AT1G62180**	**AtAPR2**	**S, Se**	**Shoots**	(Loudet et al. 2007; Chao, Baraniecka, et al. 2014)
A.thaliana	**AT1G63440**	**AtHMA5**	**Cu**	**Shoots**	(Andrés-Colás et al. 2006)
A.thaliana	**AT1G66240**	**AtAX1**	**Cu**	**Shoots**	(L.-J. Shin, Lo, and Yeh 2012)
A.thaliana	**AT1G68320**	**MYB62**	**P**	**Roots,shoots**	(Devaiah et al. 2009)
A.thaliana	**AT1G71200**	**AtCITF1**	**Cu**	**Shoots, Anthers**	(Jiapei Yan et al. 2017)
A.thaliana	**AT1G74770**	**BTSL1**	**Fe,Mn,Zn**	**Leaf**	(Hindt et al. 2017)
A.thaliana	**AT1G76430**	**PHT1;9**	**P,As**	**Roots,shoots**	(E. Remy et al. 2012)
A.thaliana	**AT1G80760**	**NIP6;1**	**B**	**Leaves,shoots**	(M. Tanaka et al. 2008)
A.thaliana	**AT1G80830**	**AtNRAMP1**	**Mn**	**Shoots,roots**	(Cailliatte et al. 2010)
A.thaliana	**AT2G01770**	**VIT1**	**Fe**	**Seed**	(S. A. Kim et al. 2006)
A.thaliana	**AT2G01980**	**SOS1/NHX7**	**Na**	**Shoots**	(Shi et al. 2003)
A.thaliana	**AT2G13540**	**ABH1**	**S**	**seeds**	(McDowell et al. 2013)
A.thaliana	**AT2G16770**	**AtbZIP23**	**Zn**	**Shoots, roots**	(Assunção et al. 2010)
A.thaliana	**AT2G19110**	**AtHMA4**	**Zn**	**Shoots,seeds**	(Hussain et al. 2004; Olsen et al. 2016)
A.thaliana	**AT2G21045**	**AtHAC1**	**As**	**Shoots**	(Chao, Chen, et al. 2014)
A.thaliana	**AT2G23150**	**AtNRAMP3**	**Fe,Mn,Zn**	**Shoots**	(Lanquar et al. 2010)
A.thaliana	**AT2G23240**	**AtMT4b**	**Cu,Zn**	**Seeds**	(Y. Ren et al. 2012)
A.thaliana	**AT2G25680**	**MOT1**	**Mo**	**Leaf**	(I. Baxter et al. 2008)

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A.thaliana	**AT2G28160**	**FRU**	**Fe**	**Shoots**	(Yuan et al. 2008)
A.thaliana	**AT2G28670**	**ESB1**	**Ca,Mn,Zn,Na,S,K,As, Se,Mo**	**Leaf**	(I. Baxter et al. 2009)
A.thaliana	**AT2G32830**	**PHT1;5**	**P**	**Roots**	(Nagarajan et al. 2011)
A.thaliana	**AT2G33770**	**PHO2**	**P**	**Roots,shoots**	(T.-Y. Liu et al. 2012)
A.thaliana	**AT2G37430**	**ZAT11**	**Ni**	**Shoots**	(X.-M. Liu et al. 2014)
A.thaliana	**AT2G38460**	**FPN1**	**Co**	**Leaf**	(Morrissey et al. 2009)
A.thaliana	**AT2G38940**	**PHT1;4**	**P**	**Roots,shoots**	(H. Shin et al. 2004)
A.thaliana	**AT2G39450**	**AtMTP11**	**Mn**	**Shoots,roots**	(Peiter et al. 2007)
A.thaliana	**AT2G42000**	**AtMT4a**	**Cu,Zn**	**Seeds**	(Y. Ren et al. 2012)
A.thaliana	**AT2G46430**	**CNGC3**	**K**	**Leaf**	(Gobert et al. 2006)
A.thaliana	**AT2G46800**	**AtMTP1**	**Zn**	**Shoots**	(Desbrosses-Fonrouge et al. 2005)
A.thaliana	**AT2G47160**	**BOR1**	**B**	**Shoots**	(Miwa, Takano, and Fujiwara 2006)
A.thaliana	**AT3G01310**	**VIH2**	**P**	**Shoots**	(Zhu et al. 2019)
A.thaliana	**AT3G06060**	**TSC10a**	**Na,K,Rb,Mg,Ca,Fe, Mo**	**Leaf**	(Chao et al. 2011)
A.thaliana	**AT3G06100**	**NIP7**	**As**	**NA**	(Lindsay and Maathuis 2016; Isayenkov and Maathuis 2008)
A.thaliana	**AT3G08040**	**FRD3/MAN1**	**Mn**	**Leaf**	(Delhaize 1996)
A.thaliana	**AT3G12750**	**AtZIP1**	**Mn**	**Roots**	(Milner et al. 2013)
A.thaliana	**AT3G12820**	**myb10**	**Fe,Cd,Zn,Co,Mo**	**Leaf**	(Palmer et al. 2013)
A.thaliana	**AT3G13320**	**CAX2**	**Mn,Fe,K,P**	**Seed**	(Connorton et al. 2012)
A.thaliana	**AT3G13405**	**mir169a**	**N**	**Root**	(M. Zhao et al. 2011)
A.thaliana	**AT3G14280**		**S**	**seeds**	(McDowell et al. 2013)
A.thaliana	**AT3G15380**	**AtCTL1**	**Na, Fe, Zn, Mn, Mo**	**Shoots, Roots**	(Gao et al. 2017)
A.thaliana	**AT3G18290**	**BTS**	**Fe,Zn,Mn**	**Leaf**	(Hindt et al. 2017)
A.thaliana	**AT3G22890**	**AtATPS1**	**S**	**Shoos**	(Koprivova et al. 2013)
A.thaliana	**AT3G23210**	**bHLH34**	**Fe**	**Root, shoot**	(X. Li et al. 2016)
A.thaliana	**AT3G23430**	**PHO1**	**P**	**Shoots**	(Khan et al. 2014)
A.thaliana	**AT3G43790**	**ZIFL2**	**Cs**	**Leaf**	(Estelle Remy et al. 2015)
A.thaliana	**AT3G47640**	**PYE**	**Fe,Zn,Mn,Co**	**Root**	(Long et al. 2010)
A.thaliana	**AT3G47950**	**AHA4**	**Na**	**Root**	(Vitart et al. 2001)
A.thaliana	**AT3G51860**	**CAX3**	**P,K**	**Seed**	(Connorton et al. 2012)
A.thaliana	**AT3G51895**	**SULTR3;1**	**S**	**Leaf**	(Cao et al. 2013)
A.thaliana	**AT3G56970**	**bHLH38**	**Fe**	**Shoots**	(Yuan et al. 2008)

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A.thaliana	**AT3G56980**	**bHLH39**	**Fe**	**Shoots**	(Yuan et al. 2008)
A.thaliana	**AT3G58060**	**AtMTP8**	**Mn**	**Shoots,seeds**	(Eroglu et al. 2016, 2017)
A.thaliana	**AT3G58810**	**AtMTP3**	**Zn**	**Shoots**	(Arrivault, Senger, and Krämer 2006)
A.thaliana	**AT3G58970**	**MGT6**	**Mg**	**Roots,shoots**	(Mao et al. 2014)
A.thaliana	**AT3G62270**	**BOR2**	**B**	**Shoots**	(Miwa et al. 2013)
A.thaliana	**AT4G02780**	**GA1**	**Fe**	**Root**	(Wild et al. 2016)
A.thaliana	**AT4G10310**	**AtHKT1;1**	**Na**	**Leaf**	(I. Baxter et al. 2010)
A.thaliana	**AT4G10380**	**NIP5;1**	**B**	**Roots,shoots**	(Takano et al. 2006)
A.thaliana	**AT4G13420**	**HAK5**	**Rb,Cs**	**Roots**	(Rubio et al. 2008; Qi et al. 2008)
A.thaliana	**AT4G14410**	**bHLH104**	**Fe**	**Root, shoot**	(X. Li et al. 2016)
A.thaliana	**AT4G16370**	**OPT3**	**Fe,Cd**	**Leaf**	(Zhai et al. 2014)
A.thaliana	**AT4G19690**	**IRT1**	**Fe,Mn,Co,Cd,Zn**	**Root**	(Eide et al. 1996)
A.thaliana	**AT4G23100**	**GSH1**	**Cd,As**	**Shoots**	(J. Guo et al. 2008)
A.thaliana	**AT4G24120**	**YSL1**	**Fe,Zn,Cu**	**NA**	(Waters et al. 2006)
A.thaliana	**AT4G28610**	**AtPHR1**	**P**	**Shoots**	(Nilsson, Müller, and Nielsen 2007)
A.thaliana	**AT4G30110**	**AtHMA2**	**Zn**	**Shoots,seeds**	(Hussain et al. 2004; Olsen et al. 2016)
A.thaliana	**AT4G30120**	**AtHMA3**	**Cd,Zn**	**Leaf**	(Chao et al. 2012; Pita-Barbosa et al. 2019)
A.thaliana	**AT4G33000**	**CBL10**	**K**	**Shoots**	(X.-L. Ren et al. 2013)
A.thaliana	**AT4G35040**	**AtbZIP19**	**Zn**	**Shoots, roots**	(Assunção et al. 2010)
A.thaliana	**AT4G37270**	**HMA1**	**Zn**	**Shoots**	(Y.-Y. Kim et al. 2009)
A.thaliana	**AT5G02600**	**NaKR1**	**Na,K,Rb**	**Leaf**	(Tian et al. 2010)
A.thaliana	**AT5G03455**	**ACR2**	**As,P**	**Roots,shoots**	(Dhankher et al. 2006)
A.thaliana	**AT5G03570**	**FPN2**	**Co,Ni**	**Leaf**	(Morrissey et al. 2009; Schaaf et al. 2006)
A.thaliana	**AT5G09690**	**MGT7**	**Mg**	**Shoots**	(Kamiya et al. 2012)
A.thaliana	**AT5G13740**	**ZIF1**	**Zn,Fe**	**Shoots**	(Haydon et al. 2012)
A.thaliana	**AT5G15070**	**VIH1**	**P**	**Shoots**	(Zhu et al. 2019)
A.thaliana	**AT5G15410**	**CNGC2/DND1**	**Ca,Mg**	**seeds**	(McDowell et al. 2013)
A.thaliana	**AT5G17290**	**APG5**	**Fe, Mn, Zn**	**Leaf, shoots, seeds**	(Pottier et al. 2019)
A.thaliana	**AT5G18830**	**AtSPL7**	**Cu**	**Shoots, roots**	(Bernal et al. 2012)
A.thaliana	**AT5G20650**	**COPT5**	**Cu**	**Shoots, roots, seeds**	(Klaumann et al. 2011)

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A.thaliana	AT5G35410	SOS2	Na	seeds	(McDowell et al. 2013)
A.thaliana	AT5G42130	AtMfl1	Fe	Leaves, shoots	(Tarantino et al. 2011)
A.thaliana	AT5G43350	PHT1;1	P,As	Shoots	(H. Shin et al. 2004; Catarecha et al. 2007)
A.thaliana	AT5G44070	PCS1	Zn,Cd,As	Leaf	(Kühnlenz et al. 2016; J. Guo et al. 2008)
A.thaliana	AT5G53130	CNGC1	Pb	Leaf	(Sunkar et al. 2000)
A.thaliana	AT5G53550	YSL3	Fe,Zn,Cu	NA	(Waters et al. 2006)
A.thaliana	AT5G54680	ILR3	Cd,Co,Fe,Mn,Zn	Leaf	(Rampey et al. 2006)
A.thaliana	AT5G54810	AtTSB1	Cd	Roots,shoots	(Sanjaya et al. 2008)
A.thaliana	AT5G57620	AtMYB36	Li, B, Na, Mg, K, Ca, Mn, Fe, Co, Ni, Cu, Zn, Rb, Sr, Mo, Cd	Shoots	(Kamiya et al. 2015)
A.thaliana	AT5G59030	COPT1	Cu	Seed,Leaf	(Sancenón et al. 2004)
A.thaliana	AT5G64930	CPR5	K	Leaf	(Borghi, Rus, and Salt 2011)
A.thaliana	AT5G67330	AtNRAMP3	Fe,Mn,Zn	Shoots	(Lanquar et al. 2010)
M.truncatula	Medtr1g010270	MtMOT1.2	Mo	Nodules	(Gil-Díez et al. 2018)
M.truncatula	Medtr3g088460	MtNramp1	Fe	Nodules	(Tejada-Jiménez et al. 2015)
M.truncatula	Medtr3g464210	MtMOT1.3	Mo	Nodules	(Tejada-Jiménez et al. 2017)
M.truncatula	Medtr4g019870	MtCOPT1	Cu	Nodules	(Senovilla et al. 2018)
M.truncatula	Medtr4g064893	MtMTP2	Zn	Nodules	(León-Mediavilla et al. 2018)
M.truncatula	Medtr4g083570	MtZIP6	Zn	Nodules	(Abreu et al. 2017)
O.sativa	LOC_Os01g03914	OsMTP9	Mn	Shoots	(Ueno et al. 2015)
O.sativa	LOC_Os01g20160	OsHKT1;5	Na	Leaf, shoots	(N. I. Kobayashi et al. 2017)
O.sativa	LOC_Os01g45990	AKT1	K	NA	(Ahmad, Mian, and Maathuis 2016)
O.sativa	LOC_Os01g64250	OsHORZ1	Fe	Shoots,seeds	(T. Kobayashi et al. 2013)
O.sativa	LOC_Os01g64890	OsMGT1	Mg,Na	Roots, shoots	(Z. C. Chen et al. 2017)
O.sativa	LOC_Os02g06290	OsHAC4	As	Seed	(Jiming Xu et al. 2017)
O.sativa	LOC_Os02g10290	OsHMA4	Cu	Roots, shoots, seeds	(Huang, Deng, et al. 2016)
O.sativa	LOC_Os02g13870	OsNIP1;1	As	Shoots	(Sun et al. 2018)
O.sativa	LOC_Os02g43370	OsYSL2	Fe,Mn	Seeds	(Ishimaru et al. 2010)
O.sativa	LOC_Os02g43410	OsYSL15	Fe	Roots, shoots, seeds	(Lee et al. 2009)
O.sativa	LOC_Os02g51110	LSI1	Se	Roots,shoots	(X. Q. Zhao et al. 2010)
O.sativa	LOC_Os02g53490	OsMTP8.2	Mn	Shoots, roots	(Takemoto et al. 2017)
O.sativa	LOC_Os02g56510	OsPHO1;2	P	Shoots	(Secco, Baumann, and Poirier 2010)

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O.sativa	**LOC_Os03g05640**	**OsPT2**	**Se**	**Roots, shoots**	(L. Zhang et al. 2014)
O.sativa	**LOC_Os03g09140**	**OsRab6a**	**Fe,Zn**	**Seeds, shoot, roots**	(Yang and Zhang 2016)
O.sativa	**LOC_Os03g12530**	**OsMTP8.1**	**Mn**	**Shoots, roots**	(Z. Chen et al. 2013)
O.sativa	**LOC_Os03g18550**	**OsMIT**	**Fe**	**Shoots**	(Bashir et al. 2011)
O.sativa	**LOC_Os03g19420**	**OsNAS2**	**Fe**	**Seeds**	(Lee et al. 2012)
O.sativa	**LOC_Os03g21240**	**OsPHR2**	**P**	**Shoots**	(Zhou et al. 2008)
O.sativa	**LOC_Os04g32920**	**OsHAK1**	**Cs**	**Shoots,seeds**	(Rai et al. 2017)
O.sativa	**LOC_Os04g38940**	**OsVIT1**	**Fe,Zn**	**Shoots,seeds**	(Yu Zhang et al. 2012)
O.sativa	**LOC_Os04g45860**	**OsYSL9**	**Fe**	**Shoots,seeds**	(Senoura et al. 2017)
O.sativa	**LOC_Os04g45900**	**OsYSL16**	**Cu**	**Roots,shoots, seeds**	(Zheng et al. 2012)
O.sativa	**LOC_Os04g46940**	**OsHMA5**	**Cu**	**Roots,shoots**	(Deng et al. 2013)
O.sativa	**LOC_Os04g52310**	**OsZIP3**	**Zn**	**Shoots**	(Sasaki et al. 2015)
O.sativa	**LOC_Os04g52900**	**OsABCC1**	**As**	**Seeds**	(Song et al. 2014)
O.sativa	**LOC_Os04g56430**	**OsRMC**	**Fe,Mn,Cu**	**Root,shoot, seeds**	(Yang et al. 2013)
O.sativa	**LOC_Os05g34290**	**OsPCS1***	**As**	**Seeds**	(Hayashi et al. 2017)
O.sativa	**LOC_Os05g39560**	**OsZIP5**	**Zn**	**Leaf**	(Lee et al. 2010)
O.sativa	**LOC_Os05g47780**	**OsHRZ2**	**Fe**	**Shoots,seeds**	(T. Kobayashi et al. 2013)
O.sativa	**LOC_Os05g48390**	**OsPHO2**	**P**	**Leaf**	(C. Wang et al. 2009)
O.sativa	**LOC_Os06g01260**	**OsPCS2***	**As, Cd**	**Seeds**	(Uraguchi et al. 2017)
O.sativa	**LOC_Os06g05160**	**SPDT**	**P**	**Seed**	(Yamaji et al. 2017)
O.sativa	**LOC_Os06g48720**	**OsHMA2**	**Zn**	**Shoots, roots**	(Takahashi et al. 2012)
O.sativa	**LOC_Os06g48810**	**OsHKT2;1**	**Na**	**Roots, shoots**	(Horie et al. 2007)
O.sativa	**LOC_Os07g01810**	**TPKb**	**K**	**Leaf, root**	(Ahmad et al. 2016)
O.sativa	**LOC_Os07g09000**	**OsPHF1**	**P**	**Leaf, root**	(J. Chen et al. 2011)
O.sativa	**LOC_Os07g12900**	**OsHMA3**	**Cd**	**Shoots,seeds**	(N. Tanaka et al. 2016)
O.sativa	**LOC_Os07g15370**	**NRAMP5**	**Fe,Mn,Cd**	**Leaf**	(Sasaki et al. 2012)
O.sativa	**LOC_Os08g01120**	**OsMOT1;1**	**Mo**	**Shoots,Seed**	(Huang et al. 2019)
O.sativa	**LOC_Os08g04390**	**OsPRI1**	**Fe**	**Shoots, roots**	(H. Zhang et al. 2017)
O.sativa	**LOC_Os08g05590**	**OsNIP3;2**	**As**	**Roots**	(Y. Chen et al. 2017)
O.sativa	**LOC_Os08g05600**	**OsNIP3;3**	**As**	**Shoots**	(Sun et al. 2018)
O.sativa	**LOC_Os08g10480**	**OsATX1**	**Cu**	**Shoots, roots, seeds**	(Yuanyuan Zhang et al. 2018)
O.sativa	**LOC_Os09g23300**	**OsVIT2**	**Fe,Zn**	**Shoots,seeds**	(Yu Zhang et al. 2012)
O.sativa	**LOC_Os12g03899**	**ZIFL12**	**Fe**	**Shoots**	(Che et al. 2019)
O.sativa	**LOC_Os12g18410**	**OsMIR**	**Fe**	**Shoots, Roots, seeds**	(Ishimaru et al. 2009)
O.sativa	**LOC_Os12g32400**	**OsbHLH133**	**Fe**	**Leaf,root, shoot**	(L. Wang et al. 2013)
O.sativa	**LOC_Os12g37840**	**OsBOR1**	**B**	**Shoots**	(Nakagawa et al. 2007)
O.sativa	**Os01g0689300**	**OsHRZ1**	**Fe**	**Shoots,seeds**	(T. Kobayashi et al. 2013)
T.aestivum	**2AL-TRIAE_CS42_ 2AL_TGACv1_095050_ AA0306410**	**TaIPK1**	**Fe, Zn**	**Seed**	(Aggarwal et al. 2018)

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T.aestivum	**Traes_4AS_7220D33B3**	**Ta-PHR1**	**P**	**Shoots**	(J. Wang et al. 2013)
T.aestivum	**Traes_4BL_7091749BF**	**TaABCC13**	**Ca**	**Seed**	(Bhati et al. 2016)
T.aestivum	**Traes_4DL_3F8034BFD**	**HKT2;1**	**Na**	**Roots**	(Laurie et al. 2002)
Z.mays	**GRMZM2G047616**	**ZmHKT1**	**Na**	**Leaf**	(M. Zhang et al. 2018)
Z.mays	**GRMZM2G060952**	**YS1**	**Fe**	**Root**	(Von Wiren et al. 1994)
Z.mays	**GRMZM2G063306**	**YS3**	**Fe**	**Leaf**	(Chan-Rodriguez and Walker 2018)
Z.mays	**GRMZM2G084779**	**ZmHAK5**	**K**	**Roots, shoots**	(Qin, Wu, and Wang 2019)
Z.mays	**GRMZM2G176209**	**TLS1**	**B**	**Shoots, roots, anthers**	(Durbak et al. 2014)

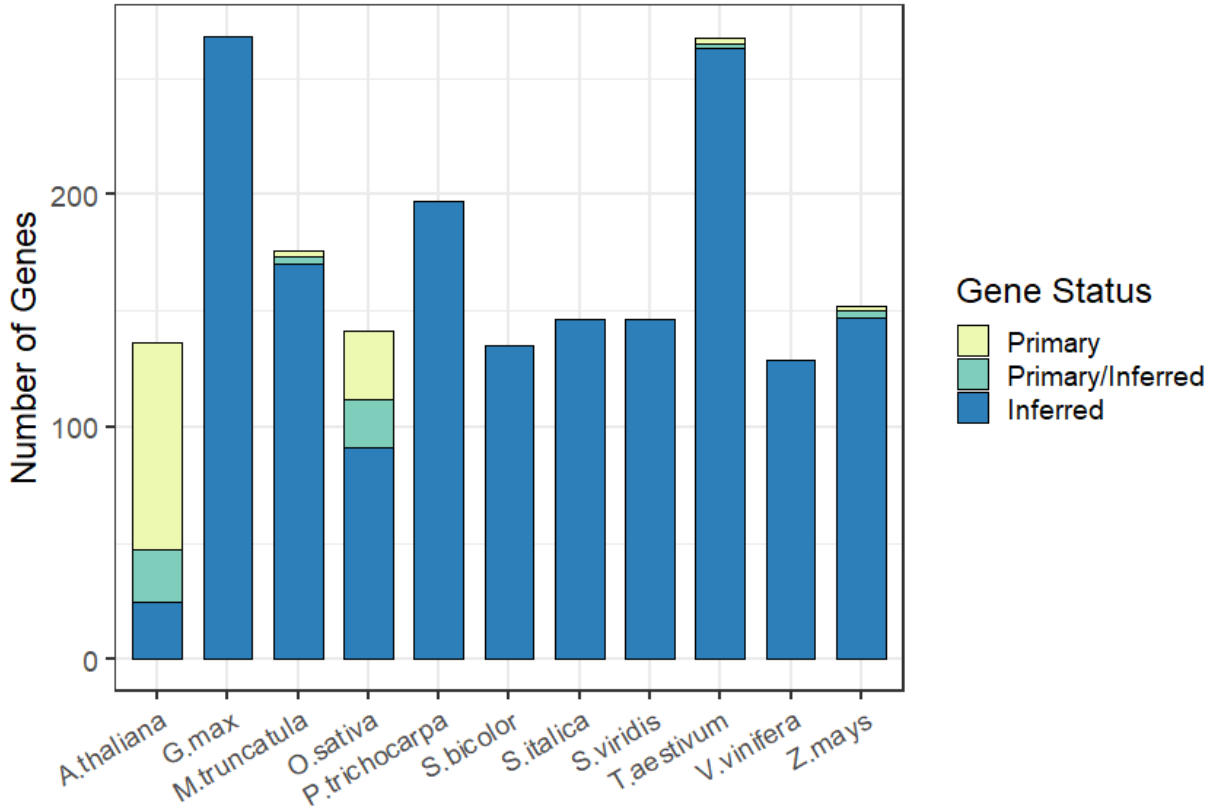

Figure 1. Number of genes for each species that are primary, inferred from other primary genes in other species, or both.

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).

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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
A.thaliana	136	65.44%	16.18%	18.38%	9.91%
O.sativa	141	20.57%	14.89%	64.54%	12.00%
M.truncatula	176	1.70%	1.70%	96.59%	0.00%
T.aestivum	267	0.75%	0.75%	98.50%	25.00%
Z.mays	152	1.32%	1.97%	96.71%	0.00%
G.max	268	0.00%	0.00%	100.00%	0.00%
P.trichocarpa	197	0.00%	0.00%	100.00%	0.00%
S.bicolor	135	0.00%	0.00%	100.00%	0.00%
S.italica	146	0.00%	0.00%	100.00%	0.00%
S.viridis	146	0.00%	0.00%	100.00%	0.00%

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 were annotated as primary/inferred genes, referencing each other (STable1). 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 (S. A. Kim et al. 2006; Yu Zhang et al. 2012), and the vacuolar Mn transporters AtMTP8 and OsMTP8 (Eroglu et al. 2016; Z. 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 in 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 (I. R. Baxter et al. 2008).

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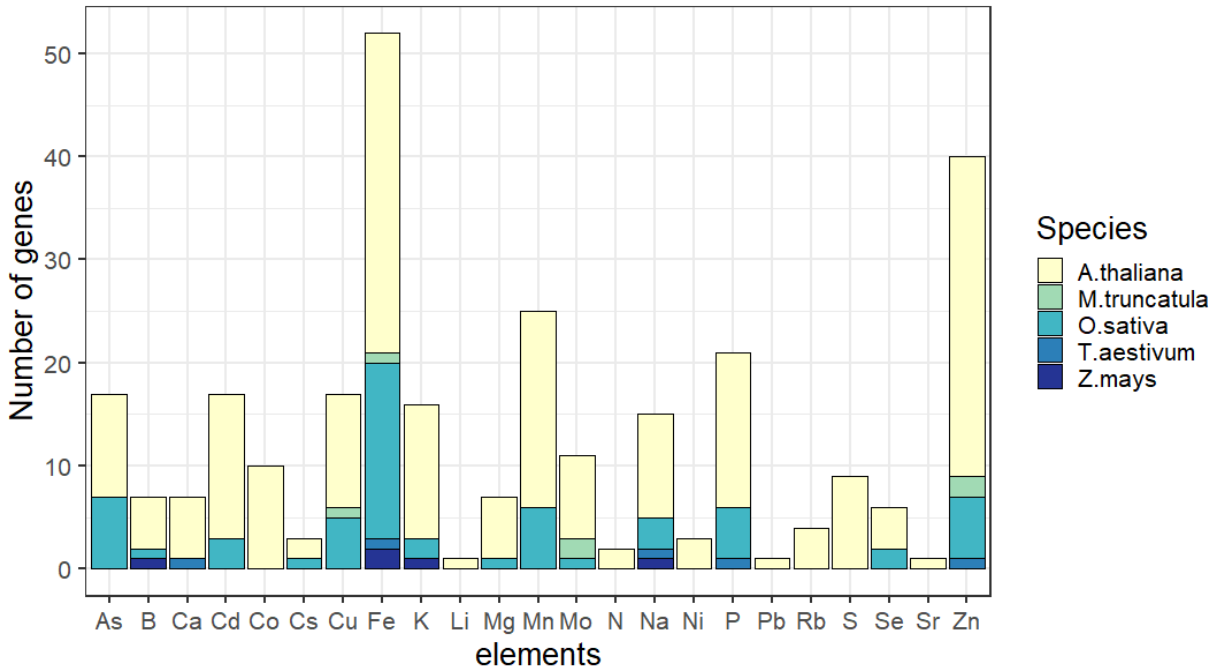

Figure 2. Number of primary genes from each species listing each element.

A. thaliana is the only species to have a primary gene listing for each element. There is a bias towards manganese, zinc and iron which have 2, 3 and 4 times more associated genes than the average 13±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 towards certain elements, our primary list is also skewed towards 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.

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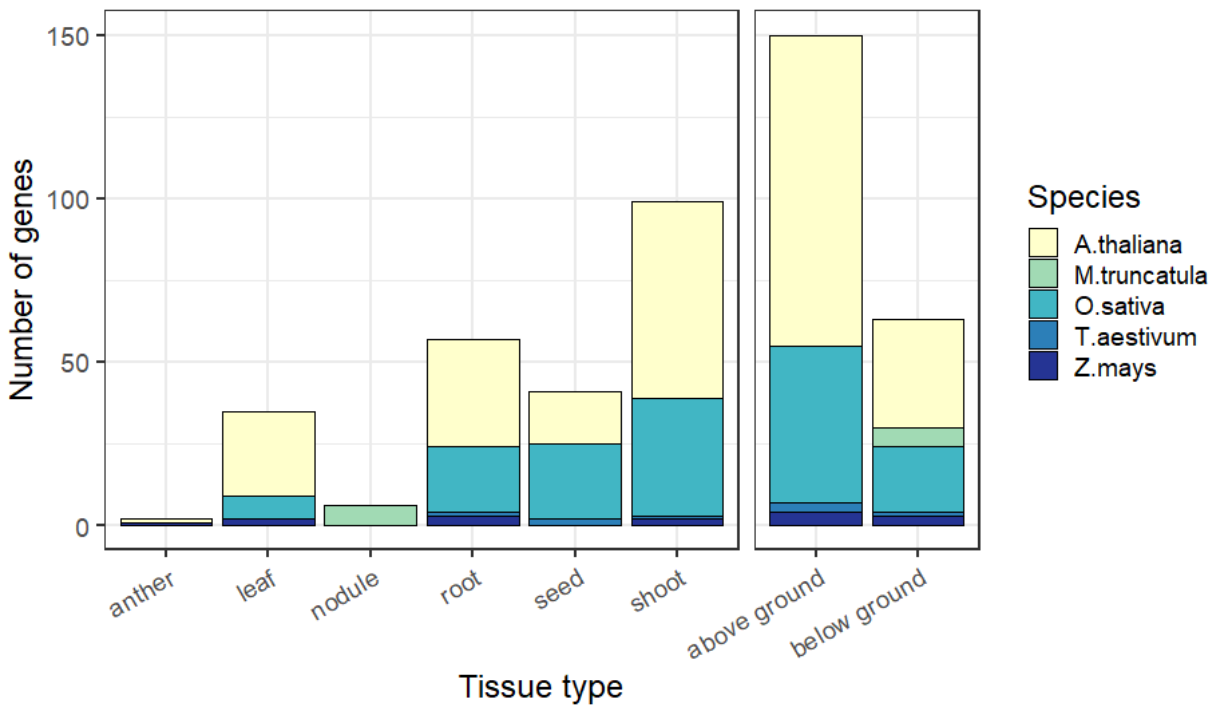

Figure 3. Number of primary genes each type of tissue contributes to the known ionome gene list. Above ground is a summary of anther, leaf, seed and shoot, while below ground is a summary of root and nodule.

Querying the manually curated PANTHER GO-slim biological process database (PANTHER v14.1, released 03-12-2019) and the GO complete biological process database (GO Ontology database, released 10-08-2019), with the *A. thaliana* KIG genes returned significantly (FDR < 0.05) overrepresented annotation terms related to the transport, response, and homeostasis of iron, 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, respectively (Waters et al. 2006; Zhai et al. 2014). Lastly, NRT1.5/NPF7.3 is also annotated as encoding an oligopeptide transporter, but Li et al. (H. Li et al. 2017) identified it as a xylem loading potassium ion antiporter.

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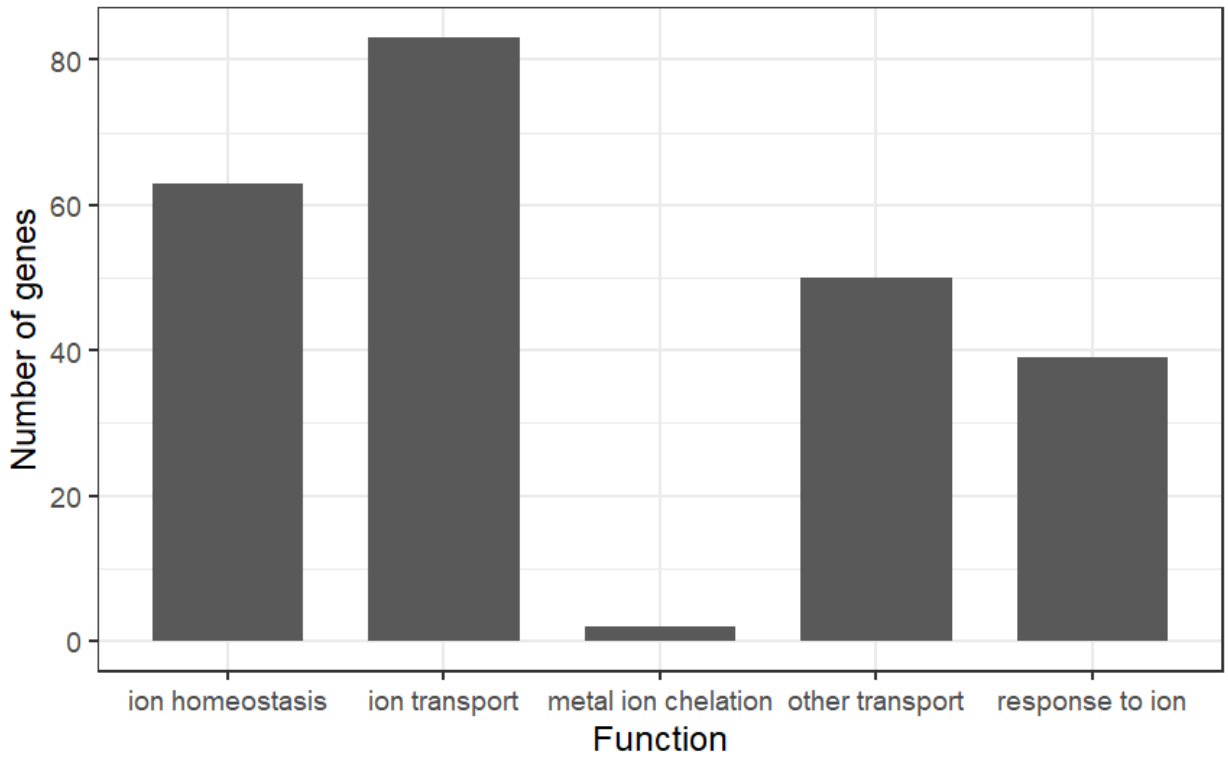

Figure 4. Known ionome genes relating to different terms from the GO complete biological process dataset. Ontology groups of GO Enrichment Analysis from PANTHER.

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 and 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 06-13-2017) 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.

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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 towards research topics (I. Baxter 2020). The list is highly enriched for 1) transporters, 2) genes that affect elemental accumulation in above ground tissues and 3) 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 to 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, Mian, and Maathuis 2016; Jiming 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.

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 or email corresponding author. KIG lists v1.0 for each of

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the species can be viewed in STable1, and future updates to the list can be found at https://docs.google.com/spreadsheets/d/1XI2l1vtVJiHrlXLeOS5yTQQnLYq7BOHpmjuC-kUejUU/edit?usp=sharing.

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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