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

#### Authors

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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,

such as *Arabidopsis thaliana* and rice (*Oryza sativa*), including Na<sup>+</sup> 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<sup>+</sup> 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 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)
<i>A.thaliana</i>	AT1G01340	CNGC10	K,Ca,Mg	Roots,shoots	(K. M. 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)

A.thaliana	AT1G08490	CPNIFS	Se,S	Roots,shoots	(Van Hoewyk et al. 2005)
A.thaliana	AT1G12640	LPCAT1	P	Leaf	(Kisko et al. 2018)
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,shoot s	(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)
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)

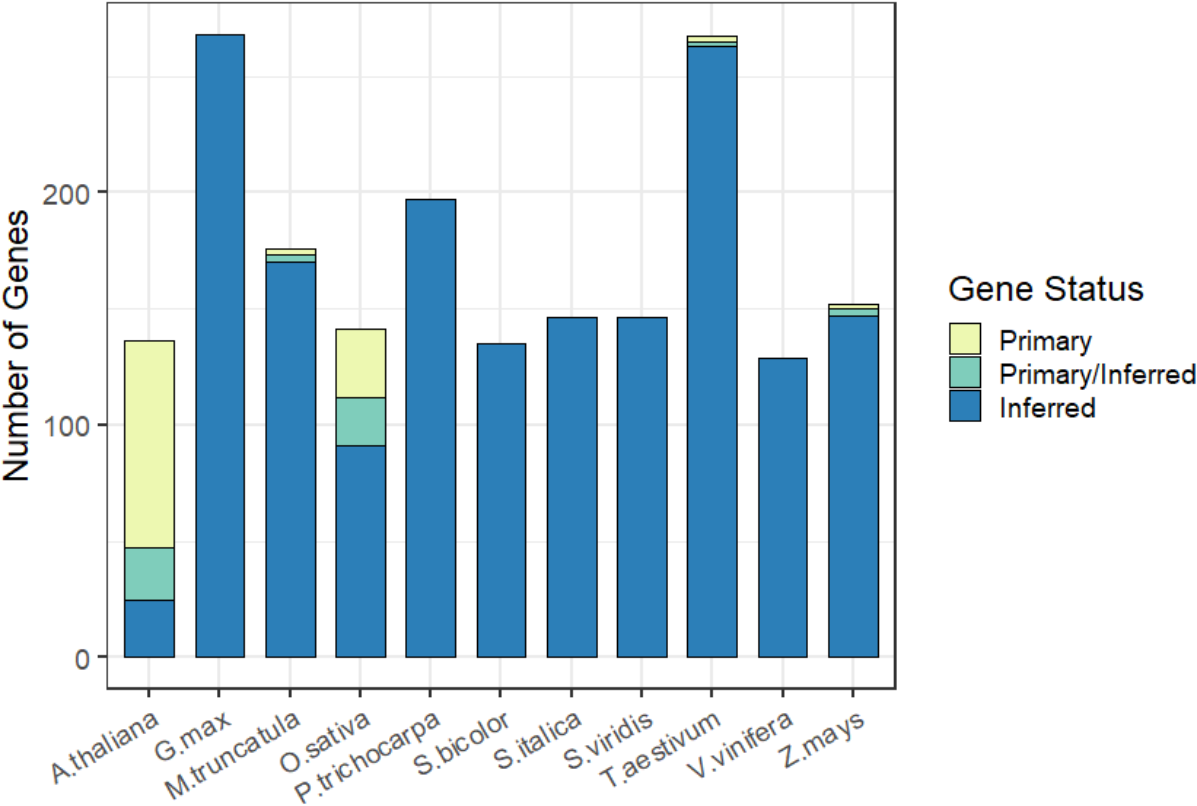
A.thaliana	AT3G51895	SULTR3;1	S	Leaf	(Cao et al. 2013)
A.thaliana	AT3G56970	bHLH38	Fe	Shoots	(Yuan et al. 2008)
A.thaliana	AT3G56980	bHLH39	Fe	Shoots	(Yuan et al. 2008)
A.thaliana	AT3G58060	AtMTP8	Mn	Shoots,seeds	(Eroglu et al. 2016, 2017)
A.thaliana	AT3G58810	AtMTP3	Zn	Shoots	(Arrivault, Senger, and 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)
A.thaliana	AT5G35410	SOS2	Na	seeds	(McDowell et al. 2013)
A.thaliana	AT5G42130	AtMf1	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)
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	OsHHLH133	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_	TalPK1	Fe, Zn	Seed	(Aggarwal et al. 2018)

	2AL_TGACv1_095050_AA0306410				
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.**

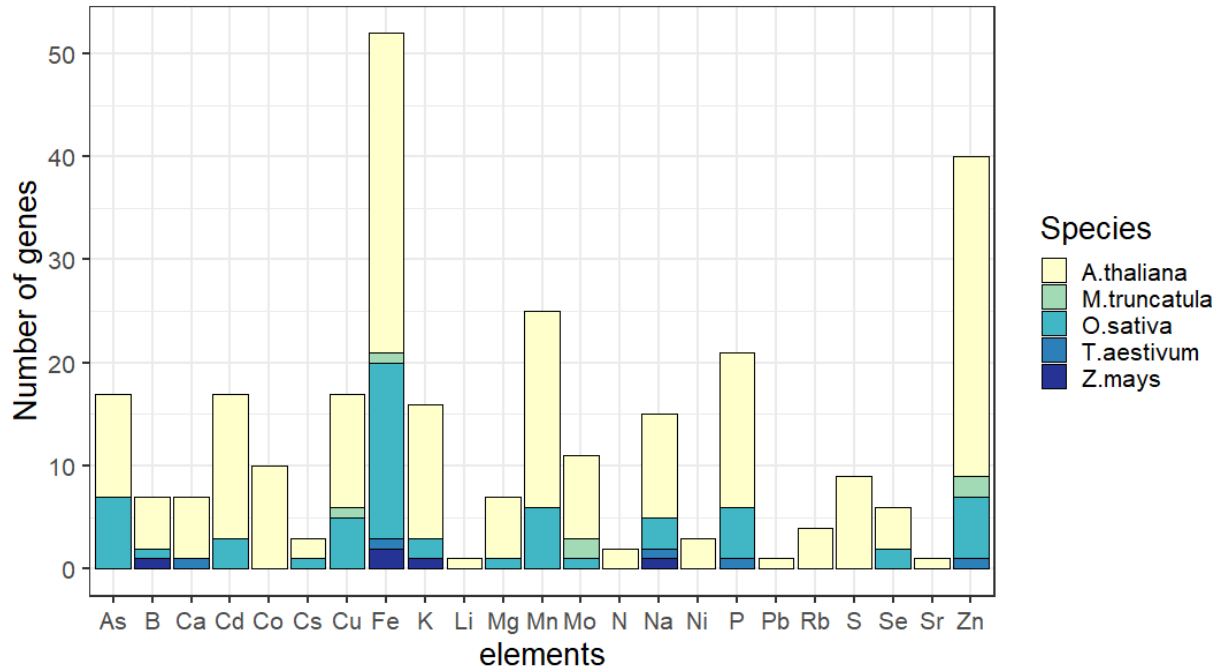
Most primary genes have orthologs in other species. Less than 10% of primary genes in *A. thaliana*, 12% in *O.sativa* and one of the four primary genes in wheat (*T. aestivum*) lack orthologs (Table 2). *G. max*, *P.trichocarpa*, *S. bicolor*, *S. italica*, and *S. viridis* currently contain only inferred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

**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%

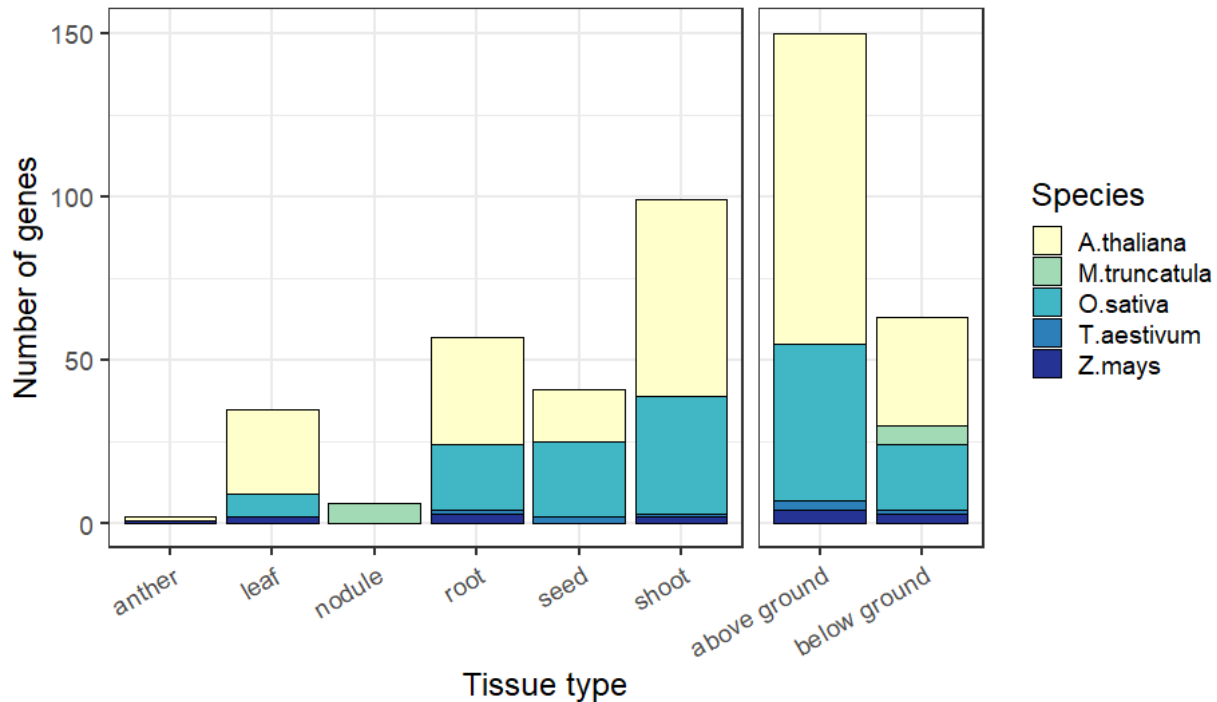
The YSL genes in *A. thaliana* and *O.sativa* are an example that provides evidence for the validity of the KIG list pipeline: AtYSL3, OsYSL9 and OsYSL16 were listed in their respective species as primary genes (Table 1) and after the ortholog search were annotated as primary/inferred genes, referencing 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).



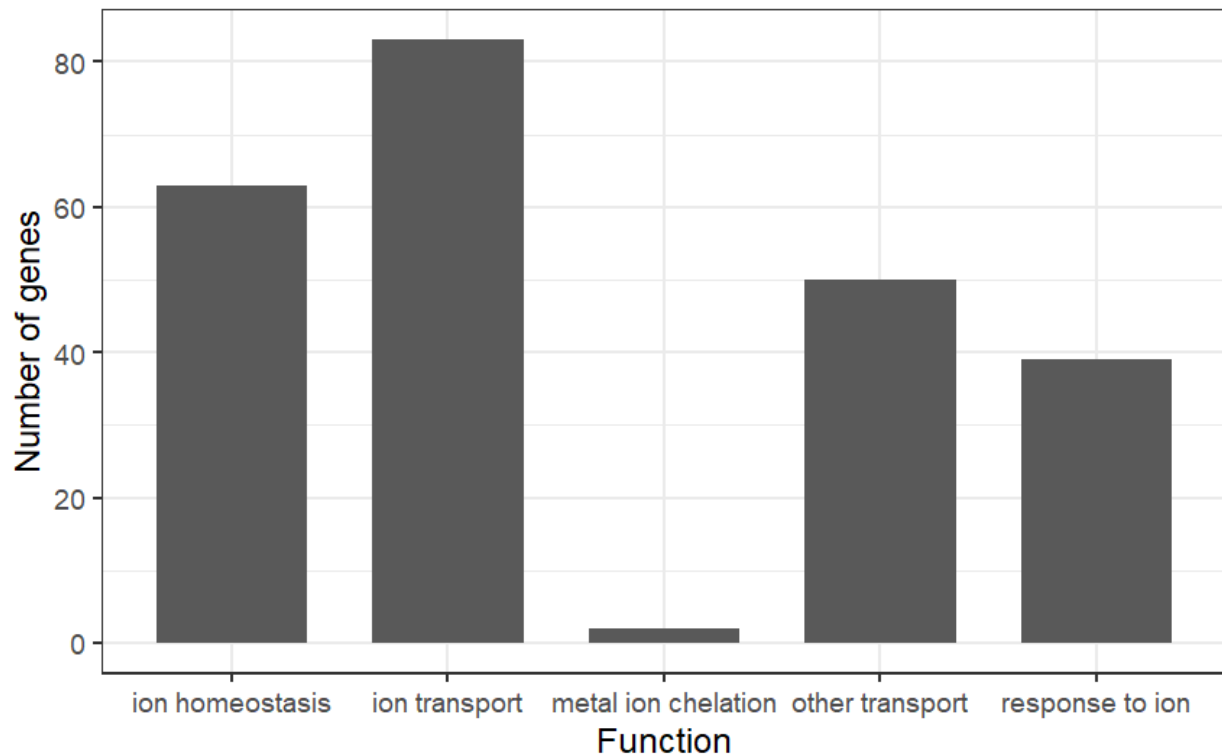
**Figure 2. Number of primary genes from each species listing each element.**

*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  $13 \pm 12$  genes of other elements. Iron is the only element to contain genes from all five species in the primary list. In addition to biases 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.



**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.



**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.

## 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](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 STable1, and future updates to the list can be found at <https://docs.google.com/spreadsheets/d/1XI2l1vtVJiHrIXLeOS5yTQQnLYq7BOHpmluC-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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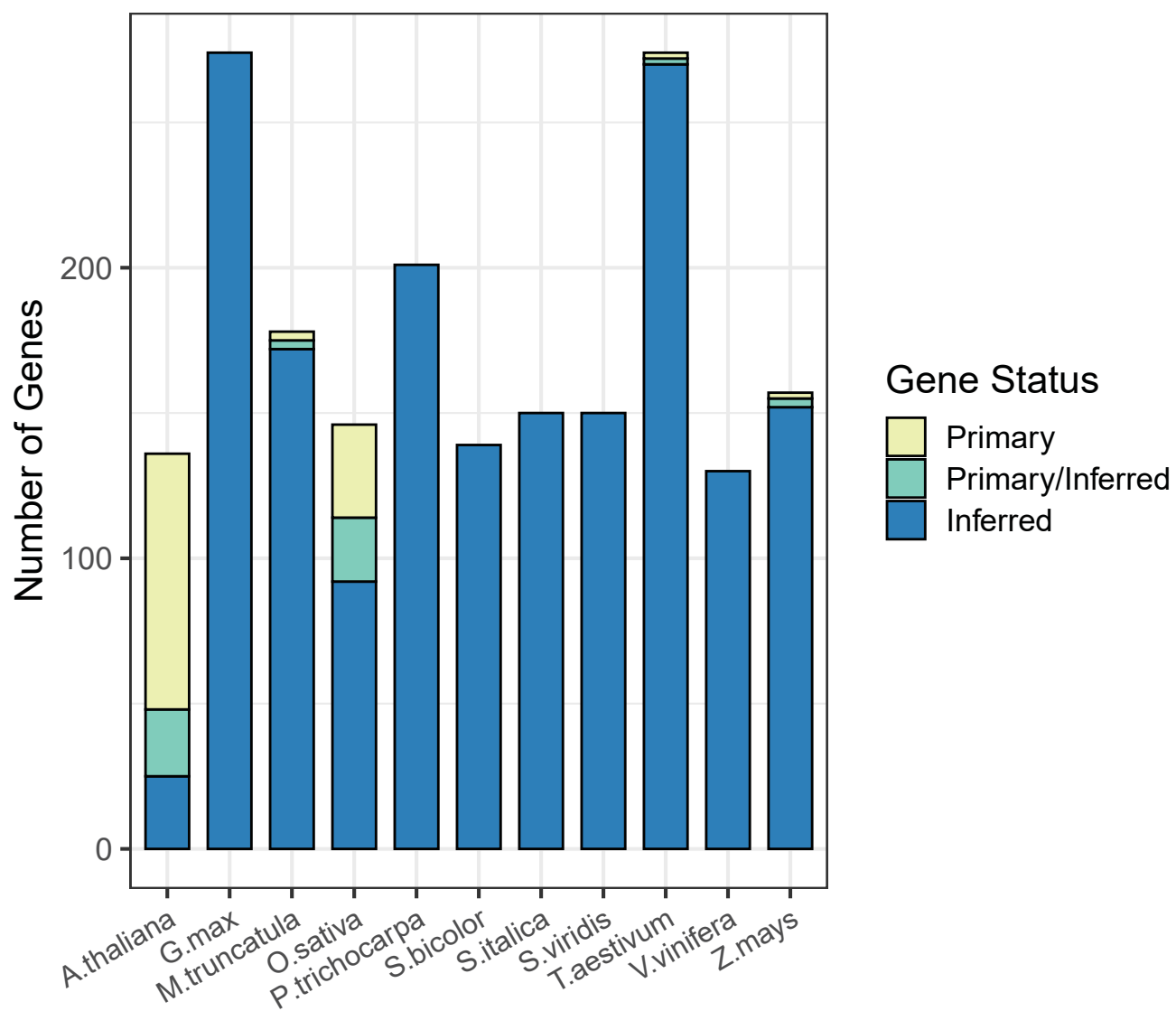
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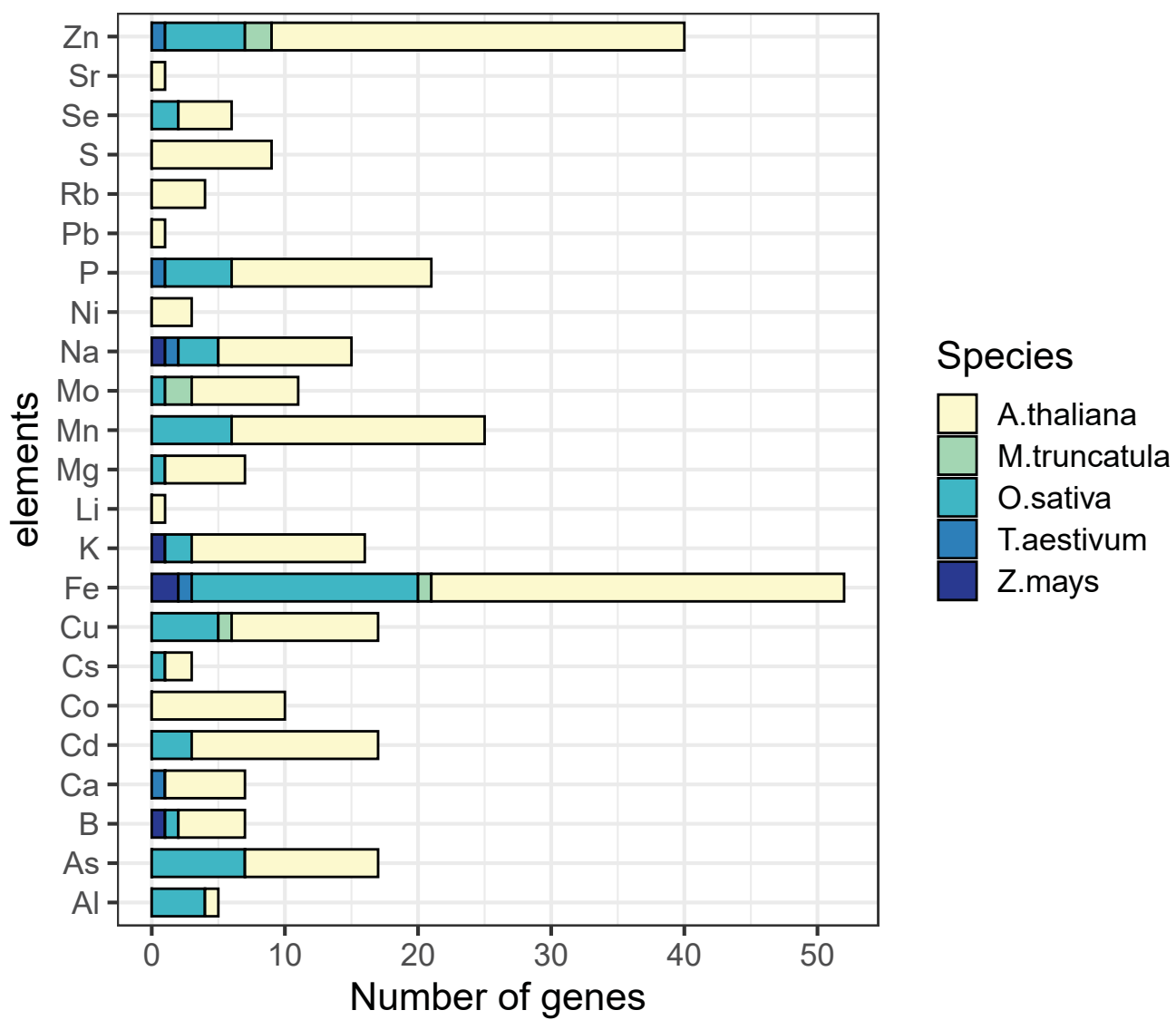
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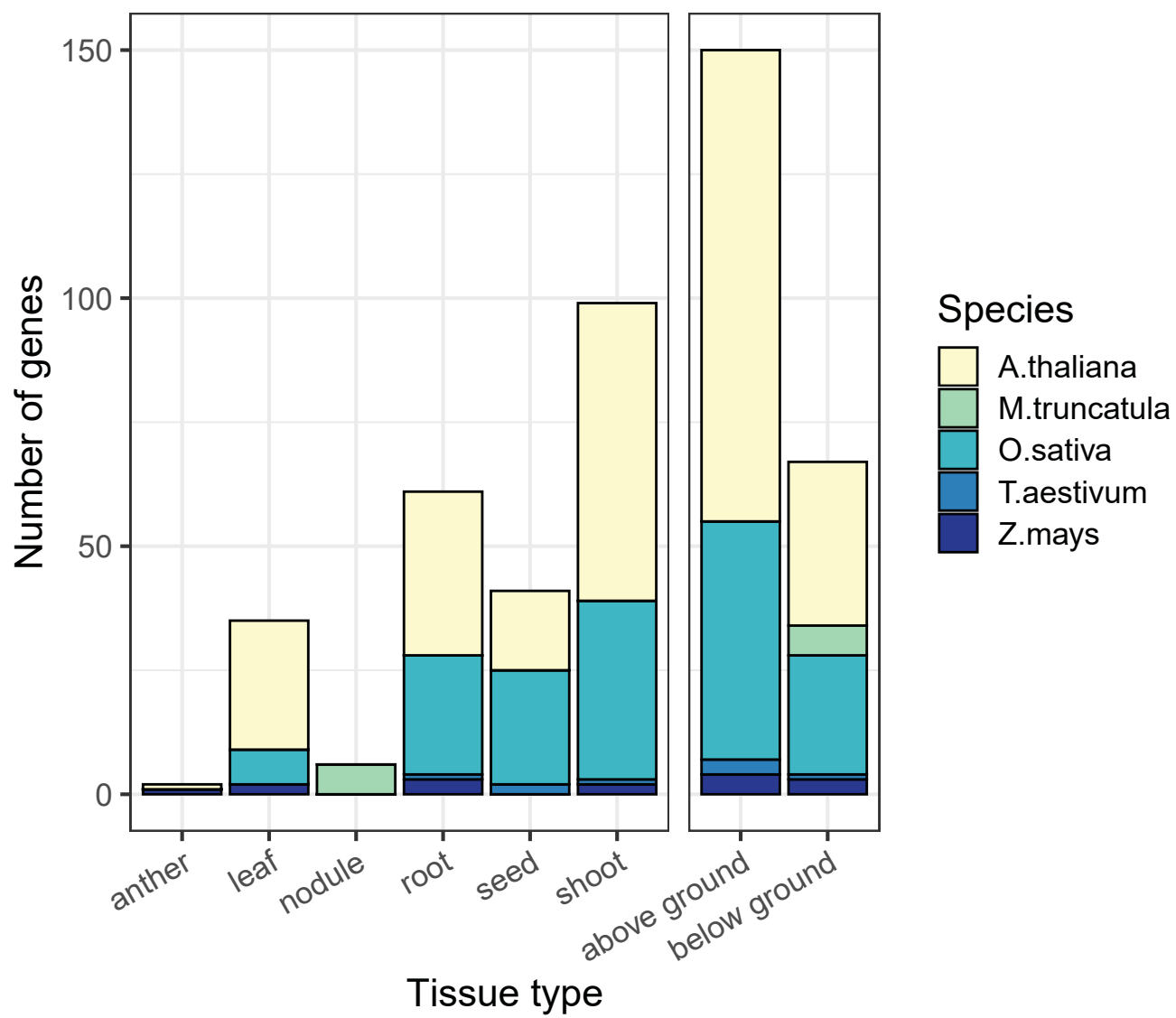
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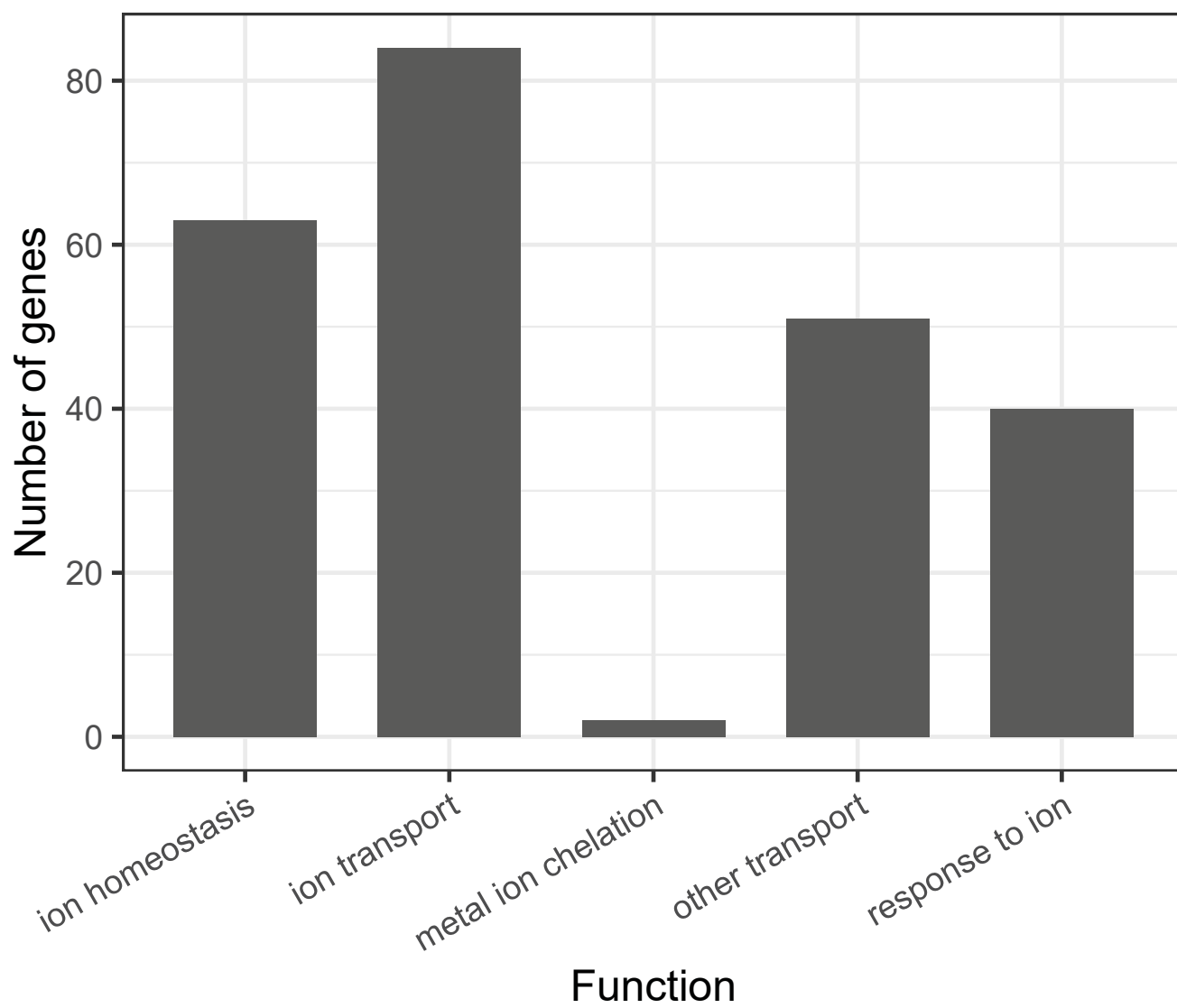












A curated list of genes that control elemental accumulation in plants.

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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 ~~476~~180 known genes ~~covering~~in 5 species, ~~23 elements~~ and their ~~1588~~1625 orthologs in 10 species. KIG covers 23 elements: aluminum, arsenic, boron, calcium, cadmium, cobalt, cesium, copper, iron, potassium, lithium, magnesium, manganese, molybdenum, sodium, nickel, phosphorous, lead, rubidium, sulfur, selenium, strontium and zinc. 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, such as *Arabidopsis thaliana* and rice (*Oryza sativa*), including Na<sup>+</sup> 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<sup>+</sup> 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, genes where the levels of the transcript are correlated with elemental accumulation, and genes involved in accumulation of organic elements, such as nitrogen. This list is focused on elements that are well-measured by inductively coupled plasma mass spectrometry (ICP-MS), such as: aluminum, arsenic, boron, calcium, cadmium, cobalt, cesium, copper, iron, potassium, lithium, magnesium, manganese, molybdenum, sodium, nickel, phosphorous, lead, rubidium, sulfur, selenium, strontium and zinc. 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 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. (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 [terms versus our primary list of genes](#). 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 [180](#) 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 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)
A.thaliana	AT1G14040	PHO1;H3	P	Shoots	(Khan et al. 2014)
A.thaliana	AT1G14870	PCR2	Zn	ShootsRoots	(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)
		<del>AtNRT1.5</del>			
		<del>AtNPF7</del>			
A.thaliana	AT1G32450	.3	K,NO3-	Shoots, Roots	(H. Li et al. 2017)
A.thaliana	AT1G36370	<del>AtMSA1</del>	S, Se	Shoots	(Huang, Chao, et al. 2016)
A.thaliana	AT1G56160	<del>myb72</del>	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	<del>AtIRT3</del>	Fe	Roots	(Lin et al. 2009)
A.thaliana	AT1G62180	<del>AtAPR2</del>	S, Se	Shoots	(Loudet et al. 2007; Chao, Baraniecka, et al. 2014)
A.thaliana	AT1G63440	<del>AtHMA5</del>	Cu	Shoots	(Andrés-Colás et al. 2006)
A.thaliana	AT1G66240	<del>AtAX1</del>	Cu	Shoots	(L.-J. Shin, Lo, and Yeh 2012)
A.thaliana	AT1G68320	MYB62	P	Roots,shoots	(Devaiah et al. 2009)
A.thaliana	AT1G71200	<del>AtGTF1</del>	Cu	Shoots, Anthers	(Jiapei Yan et al. 2017)
A.thaliana	AT1G74770	BTSL1	Fe,Mn,Zn	Leaf	(Hindt et al. 2017)

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A.thaliana	AT1G76430	PHT1;9	P,As	Roots,shoots	(E. Remy et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT1G80760	NIP6;1	B	Leaves,shoots	(M. Tanaka et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT1G80830	AtNRAMP1N RAMP1	Mn	Shoots,roots	(Cailliatte et al. 2010)	Formatted: Font: 10 pt
A.thaliana	AT2G01770	VIT1	Fe	Seed	(S. A. Kim et al. 2006)	Formatted: Font: 10 pt
A.thaliana	AT2G01980	SOS1/NHX7	Na	Shoots	(Shi et al. 2003)	Formatted: Font: 10 pt
A.thaliana	AT2G13540	ABH1	S	seeds	(McDowell et al. 2013)	Formatted: Font: 10 pt
A.thaliana	AT2G16770	AtbZIP23bZIP 23	Zn	Shoots, roots	(Assunção et al. 2010)	Formatted: Font: 10 pt
A.thaliana	AT2G19110	AtHMA4HMA 4	Zn	Shoots,seeds	(Hussain et al. 2004;Olsen et al. 2016)(Hussain et al. 2004) [Olsen et al. 2016]	Formatted: Font: 10 pt, Not Bold, Font color: Auto
A.thaliana	AT2G21045	AtHAC1HAC1 AtNRAMP3N RAMP3	As	Shoots	(Chao, Chen, et al. 2014)	Formatted: Font: 10 pt
A.thaliana	AT2G23150	AtMT4bMT4b	Fe,Mn,Zn	Shoots	(Lanquar et al. 2010)	Formatted: Font: 10 pt
A.thaliana	AT2G23240		Cu,Zn	Seeds	(Y. Ren et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT2G25680	MOT1	Mo	Leaf	(I. Baxter et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT2G28160	FRU	Fe	Shoots	(Yuan et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT2G28670	ESB1	Ca,Mn,Zn,Na,S,K,As, Se,Mo	Leaf	(I. Baxter et al. 2009)	Formatted: Font: 10 pt
A.thaliana	AT2G32830	PHT1;5	P	Roots	(Nagarajan et al. 2011)	Formatted: Font: 10 pt
A.thaliana	AT2G33770	PHO2	P	Roots,shoots	(T.-Y. Liu et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT2G37430	ZAT11	Ni	Shoots	(X.-M. Liu et al. 2014)	Formatted: Font: 10 pt
A.thaliana	AT2G38460	FPN1	Co	Leaf	(Morrissey et al. 2009)	Formatted: Font: 10 pt
A.thaliana	AT2G38940	PHT1;4	P	Roots,shoots	(H. Shin et al. 2004)	Formatted: Font: 10 pt
A.thaliana	AT2G39450	AtMTP11MTP 11	Mn	Shoots,roots Roots	(Peiter et al. 2007)	Formatted: Font: 10 pt
A.thaliana	AT2G42000	AtMT4aMT4a	Cu,Zn	Seeds	(Y. Ren et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT2G46430	CNGC3	K	Leaf	(Gobert et al. 2006)	Formatted: Font: 10 pt
A.thaliana	AT2G46800	AtMTP1MTP1	Zn	Shoots	(Desbrosses-Fonrouge et al. 2005)	Formatted: Font: 10 pt
A.thaliana	AT2G47160	BOR1	B	Shoots	(Miwa, Takano, and Fujiwara 2006)	Formatted: Font: 10 pt
A.thaliana	AT3G01310	VIH2	P	Shoots	(Zhu et al. 2019)	Formatted: Font: 10 pt
A.thaliana	AT3G06060	TSC10a	Na,K,Rb,Mg,Ca,Fe, Mo	Leaf	(Chao et al. 2011)	Formatted: Font: 10 pt
A.thaliana	AT3G06100	NIP7	As	NA	(Lindsay and Maathuis 2016; Isayenkov and Maathuis 2008)	Formatted: Font: 10 pt
A.thaliana	AT3G08040	FRD3/MAN1	Mn	Leaf	(Delhaize 1996)	Formatted: Font: 10 pt, Not Bold, No underline, Font color: Auto
A.thaliana	AT3G12750	AtZIP1ZIP1	Mn	Roots	(Milner et al. 2013)	Formatted: Font: 10 pt
A.thaliana	AT3G12820	myb10MYB10	Fe,Cd,Zn,Co,Mo	Leaf	(Palmer et al. 2013)	Formatted: Font: 10 pt



A.thaliana	AT3G13320	CAX2	Mn,Fe,K,P	Seed	(Connorton et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT3G13405	mir169a	N	Root	(M. Zhao et al. 2011)	
A.thaliana	AT3G14280		S	seeds	(McDowell et al. 2013)	Formatted: Font: 10 pt
A.thaliana	AT3G15380	<del>A</del> CTL1 <del>CTL1</del>	Na, Fe, Zn, Mn, Mo	Shoots, Roots	(Gao et al. 2017)	Formatted: Font: 10 pt
A.thaliana	AT3G18290	BTS	Fe,Zn,Mn	Leaf	(Hindt et al. 2017)	Formatted: Font: 10 pt
A.thaliana	AT3G22890	<del>A</del> ATPS1 <del>ATP</del> S1	S	Shoos	(Koprivova et al. 2013)	Formatted: Font: 10 pt, No underline, Font color: Custom Color(RGB(34,34,34))
A.thaliana	AT3G23210	bHLH34	Fe	Root, shoot	(X. Li et al. 2016)	Formatted: Font: 10 pt, Underline, Font color: Custom Color(RGB(17,85,204))
A.thaliana	AT3G23430	PHO1	P	Shoots	(Khan et al. 2014)	Formatted: Font: 10 pt, No underline, Font color: Custom Color(RGB(17,85,204))
A.thaliana	AT3G43790	ZIFL2	Cs	Leaf	(Estelle Remy et al. 2015)	Formatted: Font: 10 pt, Underline, Font color: Custom Color(RGB(17,85,204))
A.thaliana	AT3G47640	PYE	Fe,Zn,Mn,Co	Root	(Long et al. 2010)	Formatted: Font: 10 pt
A.thaliana	AT3G47950	AHA4	Na	Root	(Vitart et al. 2001)	Formatted: Font: 10 pt
A.thaliana	AT3G51860	CAX3	P,K	Seed	(Connorton et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT3G51895	SULTR3;1	S	Leaf	(Cao et al. 2013)	Formatted: Font: 10 pt
A.thaliana	AT3G56970	bHLH38	Fe	Shoots	(Yuan et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT3G56980	bHLH39	Fe	Shoots	(Yuan et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT3G58060	<del>A</del> MT <del>P8</del> MT <del>P8</del>	Mn	Shoots,seeds	(Eroglu et al. 2016, 2017)	Formatted: Font: 10 pt
A.thaliana	AT3G58810	<del>A</del> MT <del>P3</del> MT <del>P3</del>	Zn	Shoots	(Arrivault, Senger, and Krämer 2006)	Formatted: Font: 10 pt, Font color: Custom Color(RGB(34,34,34))
A.thaliana	AT3G58970	MGT6	Mg	<del>Roots,shoots</del> Shoots	(Mao et al. 2014)	Formatted: Font: 10 pt, Font color: Auto
A.thaliana	AT3G62270	BOR2	B	Shoots	(Miwa et al. 2013)(Miwa, Takano, and Fujiwara 2006)	Formatted: Font: 10 pt
A.thaliana	AT4G02780	GA1	Fe	Root	(Wild et al. 2016)	Formatted: Font: 10 pt
A.thaliana	AT4G10310	<del>A</del> HKT1 <del>HKT1</del> ;1	Na	Leaf	(I. Baxter et al. 2010)	Formatted: Font: 10 pt, Not Bold, Font color: Auto
A.thaliana	AT4G10380	NIP5;1	B	Roots,shoots	(Takano et al. 2006)	Formatted: Font: 10 pt
A.thaliana	AT4G13420	HAK5	Rb,Cs	Roots	(Rubio et al. 2008; Qi et al. 2008)(Rubio et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT4G14410	bHLH104	Fe	Root, shoot	(X. Li et al. 2016)	Formatted: Font: 10 pt
A.thaliana	AT4G16370	OPT3	Fe,Cd	Leaf	(Zhai et al. 2014)	Formatted: Font: 10 pt
A.thaliana	AT4G18910	NIP1;2	Al	Roots	(Y. Wang et al. 2017)	Formatted: Font: 10 pt
A.thaliana	AT4G19690	IRT1	Fe,Mn,Co,Cd,Zn	Root	(Eide et al. 1996)	Formatted: Font: 10 pt
A.thaliana	AT4G23100	GSH1	Cd,As	Shoots	(J. Guo et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT4G24120	YSL1	Fe,Zn,Cu	NA	(Waters et al. 2006)	Formatted: Font: 10 pt
A.thaliana	AT4G28610	<del>A</del> PHR1 <del>PHR1</del>	P	Shoots	(Nilsson, Müller, and Nielsen 2007)	Formatted: Font: 10 pt
A.thaliana	AT4G30110	<del>A</del> HMA2 <del>HMA</del> 2	Zn	Shoots,seeds	(Hussain et al. 2004; Olsen et al. 2016)	Formatted: Font: 10 pt, Not Bold, Font color: Auto

A.thaliana	AT4G30120	<del>AtHMA3</del> <del>HMA3</del>	Cd, <del>Zn</del>	Leaf	(Chao et al. 2012; Pita-Barbosa et al. 2019)	Formatted: Font: 10 pt
A.thaliana	AT4G33000	CBL10	K	Shoots	(X.-L. Ren et al. 2013)	Formatted: Font: 10 pt
A.thaliana	AT4G35040	<del>AtbZIP19</del> <del>bZIP19</del>	Zn	Shoots, roots	(Assunção et al. 2010)	Formatted: Font: 10 pt
A.thaliana	AT4G37270	HMA1	Zn	Shoots	(Y.-Y. Kim et al. 2009)	Formatted: Font: 10 pt
A.thaliana	AT5G02600	NaKR1	Na,K,Rb	Leaf	(Tian et al. 2010)	Formatted: Font: 10 pt
A.thaliana	AT5G03455	ACR2	As,P	Roots,shoots	(Dhankher et al. 2006)	Formatted: Font: 10 pt
A.thaliana	AT5G03570	FPN2	Co, <del>Ni</del>	Leaf	<del>(Morrissey et al. 2009; Schaaf et al. 2006)</del> (Morrissey et al. 2009)	Formatted: Font: 10 pt
A.thaliana	AT5G09690	MGT7	Mg	Shoots	(Kamiya et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT5G13740	ZIF1	Zn,Fe	Shoots	(Haydon et al. 2012)	Formatted: Font: 10 pt, Not Bold, Font color: Auto
A.thaliana	AT5G15070	VIH1	P	Shoots	(Zhu et al. 2019)	Formatted: Font: 10 pt
A.thaliana	AT5G15410	CNGC2/DND1	Ca,Mg	seeds	(McDowell et al. 2013)	Formatted: Font: 10 pt
A.thaliana	AT5G17290	APG5	Fe, Mn, Zn	Leaf, shoots, seeds	(Pottier et al. 2019)	Formatted: Font: 10 pt
A.thaliana	AT5G18830	<del>AtSPL7</del> <del>SPL7</del>	Cu	Shoots, roots	(Bernal et al. 2012)	Formatted: Font: 10 pt
A.thaliana	AT5G20650	COPT5	Cu	Shoots, <del>roots</del> , Roots,seeds	(Klaumann et al. 2011)	Formatted: Font: 10 pt
A.thaliana	AT5G35410	SOS2	Na	seeds	(McDowell et al. 2013)	Formatted: Font: 10 pt
A.thaliana	AT5G42130	<del>AtM#1</del> <del>M#1</del>	Fe	Leaves, shoots	(Tarantino et al. 2011)	Formatted: Font: 10 pt
A.thaliana	AT5G43350	PHT1;1	P,As	Shoots	(H. Shin et al. 2004; Catarcha et al. 2007)	
A.thaliana	AT5G44070	PCS1	Zn,Cd, <del>As</del>	Leaf	<del>(Kühnlenz et al. 2016; J. Guo et al. 2008)</del> (Kühnlenz et al. 2016)	Formatted: Font: 10 pt
A.thaliana	AT5G53130	CNGC1	Pb	Leaf	(Sunkar et al. 2000)	Formatted: Font: 10 pt
A.thaliana	AT5G53550	YSL3	Fe,Zn,Cu	NA	(Waters et al. 2006)	Formatted: Font: 10 pt
A.thaliana	AT5G54680	ILR3	Cd,Co,Fe,Mn,Zn	Leaf	(Rampey et al. 2006)	Formatted: Font: 10 pt
A.thaliana	AT5G54810	<del>AtTSB1</del> <del>TSB1</del>	Cd	Roots,shoots	(Sanjaya et al. 2008)	Formatted: Font: 10 pt
A.thaliana	AT5G57620	<del>AtMYB36</del> <del>MYB36</del>	Li, B, Na, Mg, K, Ca, Mn, Fe, Co, Ni, Cu, Zn, Rb, Sr, Mo, Cd	Shoots	(Kamiya et al. 2015)	Formatted: Font: 10 pt
A.thaliana	AT5G59030	COPT1	Cu	Seed,Leaf	(Sancenón et al. 2004)	Formatted: Font: 10 pt
A.thaliana	AT5G64930	CPR5	K	Leaf	(Borghi, Rus, and Salt 2011)	Formatted: Font: 10 pt
A.thaliana	AT5G67330	<del>AtNRAMP3</del> <del>NRAMP3</del>	Fe,Mn,Zn	Shoots	(Lanquar et al. 2010)	Formatted: Font: 10 pt
M.truncatula	Medtr1g010270	<del>MtMOT1</del> <del>MOT1</del>	Mo	Nodules	(Gil-Díez et al. 2018)	Formatted: Font: 10 pt
M.truncatula	Medtr3g088460	<del>MtNramp1</del> <del>NRAMP1</del>	Fe	Nodules	(Tejada-Jiménez et al. 2015)	Formatted: Font: 10 pt

M.truncatula	Medtr3g464210	MtMOT1MOT1.3	Mo	Nodules	(Tejada-Jiménez et al. 2017)
M.truncatula	Medtr4g019870	MtGOPT1COPT1	Cu	Nodules	(Senovilla et al. 2018)
M.truncatula	Medtr4g064893	MtMTP2MTP2	Zn	Nodules	(León-Mediavilla et al. 2018)
M.truncatula	Medtr4g083570	MtZIP6ZIP6	Zn	Nodules	(Abreu et al. 2017)
O.sativa	LOC_Os01g03914	OsMTP9MTP9	Mn	Shoots	(Ueno et al. 2015)
O.sativa	LOC_Os01g08300	CDT3	Al	Roots	(Xia, Yamaji, and Ma 2013)
O.sativa	LOC_Os01g20160	OsHKT1HKT1.5	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	OsHORZ1HORZ1	Fe	Shoots, seeds	(T. Kobayashi et al. 2013)
O.sativa	LOC_Os01g64890	OsMGT1MGT1	Mg,Na	Roots, shoots	(Z. C. Chen et al. 2017)
O.sativa	LOC_Os02g03900	NRAMP4	Al	Roots	(Xia et al. 2010)
O.sativa	LOC_Os02g06290	OsHAC4HAC4	As	Seed	(Jiming Xu et al. 2017)
O.sativa	LOC_Os02g10290	OsHMA4HMA4	Cu	Roots, shoots, seeds	(Huang, Deng, et al. 2016)
O.sativa	LOC_Os02g13870	OsNIP1NIP1.1	As	Shoots	(Sun et al. 2018)
O.sativa	LOC_Os02g43370	OsYSL2YSL2	Fe,Mn	Seeds	(Ishimaru et al. 2010)
O.sativa	LOC_Os02g43410	OsYSL15YSL15	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	OsMTP8MTP8.2	Mn	Shoots, roots	(Takemoto et al. 2017)
O.sativa	LOC_Os02g56510	OsPHO1PHO1.2	P	Shoots	(Secco, Baumann, and Poirier 2010)
O.sativa	LOC_Os03g05640	OsPT2PT2	Se	Roots, shoots	(L. Zhang et al. 2014)
O.sativa	LOC_Os03g09140	OsRab6aRab6a	Fe,Zn	Seeds, shoot, roots	(Yang and Zhang 2016)
O.sativa	LOC_Os03g12530	OsMTP8MTP8.1	Mn	Shoots, roots	(Z. Chen et al. 2013)
O.sativa	LOC_Os03g18550	OsMITMIT	Fe	Shoots	(Bashir et al. 2011)
O.sativa	LOC_Os03g19420	OsNAS2NAS2	Fe	Seeds	(Lee et al. 2012)
O.sativa	LOC_Os03g21240	OsPHR2PHR2	P	Shoots	(Zhou et al. 2008)
O.sativa	LOC_Os04g32920	OsHAK1HAK1	Cs	Shoots, seeds	(Rai et al. 2017)
O.sativa	LOC_Os04g38940	OsVIT1VIT1	Fe,Zn	Shoots,seeds	(Yu Zhang et al. 2012)
O.sativa	LOC_Os04g45860	OsYSL9YSL9	Fe	Shoots,seeds	(Senoura et al. 2017)

O.sativa	LOC_Os04g45900	<a href="#">OsYSL16YSL16</a>	Cu	Roots,shoots, seeds	(Zheng et al. 2012)	Formatted: Font: 10 pt
O.sativa	LOC_Os04g46940	<a href="#">OsHMA5HMA5</a>	Cu	Roots,shoots	(Deng et al. 2013)	Formatted: Font: 10 pt
<a href="#">O.sativa</a>	<a href="#">LOC_Os04g49410</a>	<a href="#">EXPA10</a>	<a href="#">Al</a>	<a href="#">Roots</a>	<a href="#">(Che et al. 2016)</a>	
O.sativa	LOC_Os04g52310	<a href="#">OsZIP3ZIP3</a>	Zn	Shoots	(Sasaki et al. 2015)	Formatted: Font: 10 pt
O.sativa	LOC_Os04g52900	<a href="#">OsABCC1ABCC1</a>	As	Seeds	(Song et al. 2014)	Formatted: Font: 10 pt
O.sativa	LOC_Os04g56430	<a href="#">OsRMCRCMC</a>	Fe,Mn,Cu	Root,shoot, seeds	(Yang et al. 2013)	Formatted: Font: 10 pt
O.sativa	LOC_Os05g34290	<a href="#">OsPCS1*PCS1</a>	As	Seeds	(Hayashi et al. 2017)	Formatted: Font: 10 pt
<a href="#">O.sativa</a>	<a href="#">LOC_Os05g37470</a>	<a href="#">AUX3</a>	<a href="#">Al</a>	<a href="#">Roots</a>	<a href="#">(M. Wang et al. 2019)</a>	
O.sativa	LOC_Os05g39560	<a href="#">OsZIP5ZIP5</a>	Zn	Leaf	(Lee et al. 2010)	Formatted: Font: 10 pt
O.sativa	LOC_Os05g47780	<a href="#">OsHRZ2HRZ2</a>	Fe	Shoots, seeds	(T. Kobayashi et al. 2013)	Formatted: Font: 10 pt
O.sativa	LOC_Os05g48390	<a href="#">OsPHO2PHO2</a>	P	Leaf	(C. Wang et al. 2009)	Formatted: Font: 10 pt
O.sativa	LOC_Os06g01260	<a href="#">OsPCS2*PCS2</a>	As, Cd	Seeds	(Uraguchi et al. 2017)	Formatted: Font: 10 pt
O.sativa	LOC_Os06g05160	SPDT	P	Seed	(Yamaji et al. 2017)	Formatted: Font: 10 pt
O.sativa	LOC_Os06g48720	<a href="#">OsHMA2HMA2</a>	Zn	Shoots, <a href="#">rootsRoots</a>	(Takahashi et al. 2012)	Formatted: Font: 10 pt
O.sativa	LOC_Os06g48810	<a href="#">OsHKT2HKT2</a>	Na	Roots, shoots	(Horie et al. 2007)	Formatted: Font: 10 pt
O.sativa	LOC_Os07g01810	TPKb	K	Leaf, root	(Ahmad et al. 2016)	Formatted: Font: 10 pt
O.sativa	LOC_Os07g09000	<a href="#">OsPHF1PHF1</a>	P	Leaf, root	(J. Chen et al. 2011)	Formatted: Font: 10 pt
O.sativa	LOC_Os07g12900	<a href="#">OsHMA3HMA3</a>	Cd	Shoots,seeds	(N. Tanaka et al. 2016)	Formatted: Font: 10 pt
O.sativa	LOC_Os07g15370	NRAMP5	Fe,Mn,Cd	Leaf	(Sasaki et al. 2012)	Formatted: Font: 10 pt
O.sativa	LOC_Os08g01120	<a href="#">OsMOT1MOT1</a>	Mo	Shoots,Seed	(Huang et al. 2019)	Formatted: Font: 10 pt
O.sativa	LOC_Os08g04390	<a href="#">OsPRI4PRI1</a>	Fe	Shoots, roots	(H. Zhang et al. 2017)	Formatted: Font: 10 pt
O.sativa	LOC_Os08g05590	<a href="#">OsNIP3NIP3</a>	As	Roots	(Y. Chen et al. 2017)	Formatted: Font: 10 pt
O.sativa	LOC_Os08g05600	<a href="#">OsNIP3NIP3</a>	As	Shoots	(Sun et al. 2018)	Formatted: Font: 10 pt
O.sativa	LOC_Os08g10480	<a href="#">OsATX1ATX1</a>	Cu	Shoots, <a href="#">roots, seedsRoots, Seeds</a>	(Yuan Yuan Zhang et al. 2018)	Formatted: Font: 10 pt
O.sativa	LOC_Os09g23300	<a href="#">OsVIT2VIT2</a>	Fe,Zn	Shoots,seeds	(Yu Zhang et al. 2012)	Formatted: Font: 10 pt
O.sativa	LOC_Os12g03899	ZIFL12	Fe	Shoots	(Che et al. 2019)	Formatted: Font: 10 pt
O.sativa	LOC_Os12g18410	<a href="#">OsMIRMIR</a>	Fe	Shoots, Roots, seeds	(Ishimaru et al. 2009)	Formatted: Font: 10 pt
O.sativa	LOC_Os12g32400	<a href="#">OsbHLH133bHLH133</a>	Fe	Leaf,root, shoot	(L. Wang et al. 2013)	Formatted: Font: 10 pt
O.sativa	LOC_Os12g37840	<a href="#">OsBOR1BOR1</a>	B	Shoots	(Nakagawa et al. 2007)	Formatted: Font: 10 pt
O.sativa	Os01g0689300	<a href="#">OsHRZ1HRZ1</a>	Fe	Shoots,	(T. Kobayashi et al. 2013)	Formatted: Font: 10 pt

					seeds	
T.aestivum	2AL-TRIAE_CS42_2AL_TGACv1_095050_AA0306410	TaIPK1IPK1	Fe, Zn	Seed	(Aggarwal et al. 2018)	
T.aestivum	Traes_4AS_7220D33B3	Ta-PHR1	P	Shoots	(J. Wang et al. 2013)	
T.aestivum	Traes_4BL_7091749BF	TaABCC13ABCC13	Ca	Seed	(Bhati et al. 2016)	
T.aestivum	Traes_4DL_3F8034BFD	HKT2;1	Na	Roots	(Laurie et al. 2002)	
Z.mays	GRMZM2G047616	ZmHKT1HKT1	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	ZmHAK5HAK5	K	Roots, shoots	(Qin, Wu, and Wang 2019)	
Z.mays	GRMZM2G176209	TLS1	B	Shoots, roots, anthers	(Durbak et al. 2014)	

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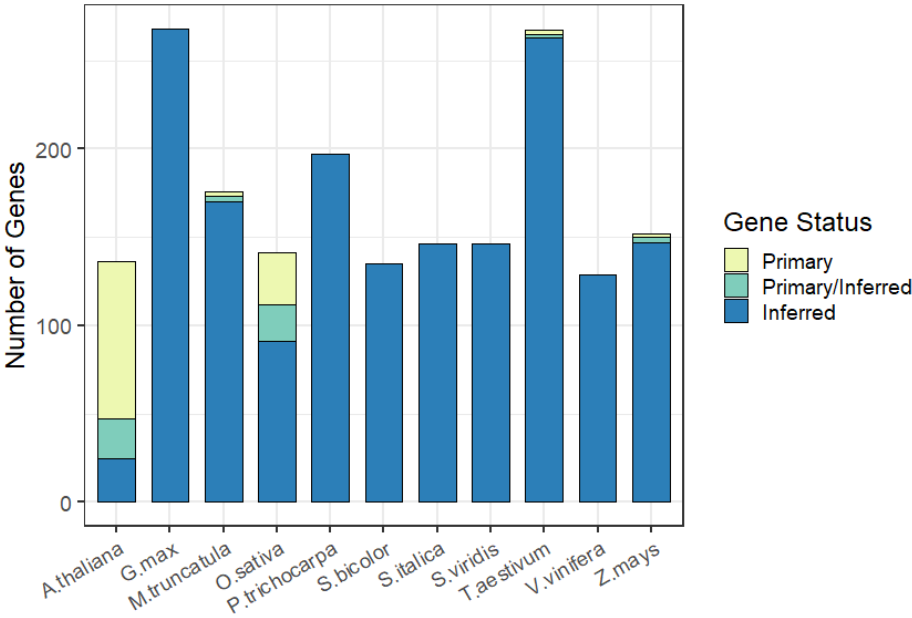
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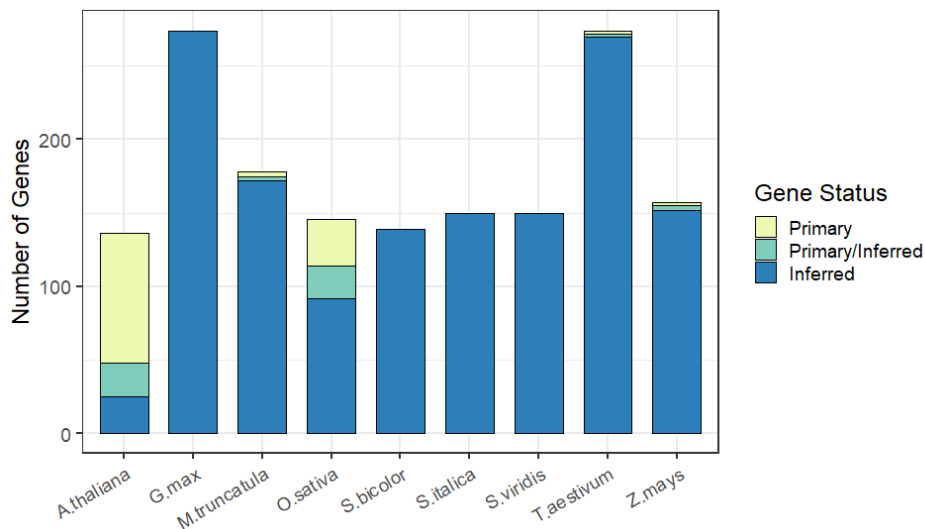
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**Figure 1. Number of genes for each species that are primary, inferred from other primary genes in other species, or both.**

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).

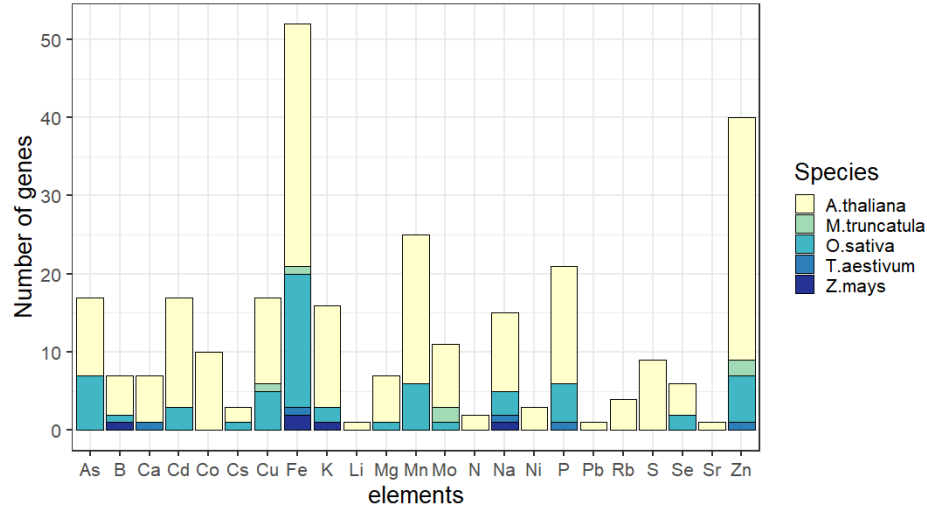
Species	Total Genes	Primary Genes	Primary/Inferred Genes	Inferred Genes	Primary & Primary/ Inferred Genes withoutw/o orthologs
A.thaliana	136	65.4464.71%	16.4891%	18.38%	9.9401%
O.sativa	144146	20.5721.92%	14.8915.07%	64.5463.01%	12.0011.11%
M.truncatula	176178	1.7069%	1.7069%	96.5963%	0.00%
T.aestivum	267274	0.7573%	0.7573%	98.5054%	25.00%
Z.mays	152157	1.3227%	1.9791%	96.7182%	0.00%
G.max*	268274	0.00%	0.00%	100.00%	0.00%
P.trichocarpa*	197201	0.00%	0.00%	100.00%	0.00%
S.bicolor*	135139	0.00%	0.00%	100.00%	0.00%

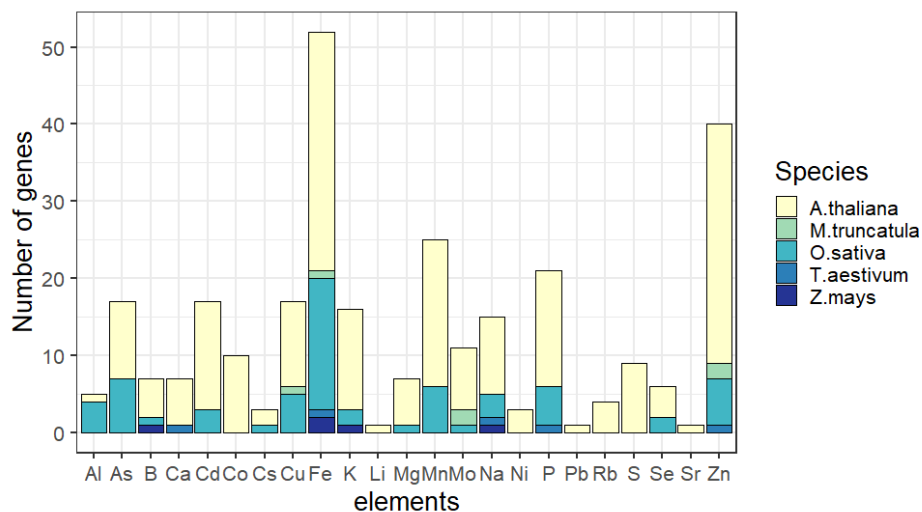
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S.italica*	<a href="#">146150</a>	0.00%	0.00%	100.00%	0.00%
S.viridis*	<a href="#">146150</a>	0.00%	0.00%	100.00%	0.00%

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).

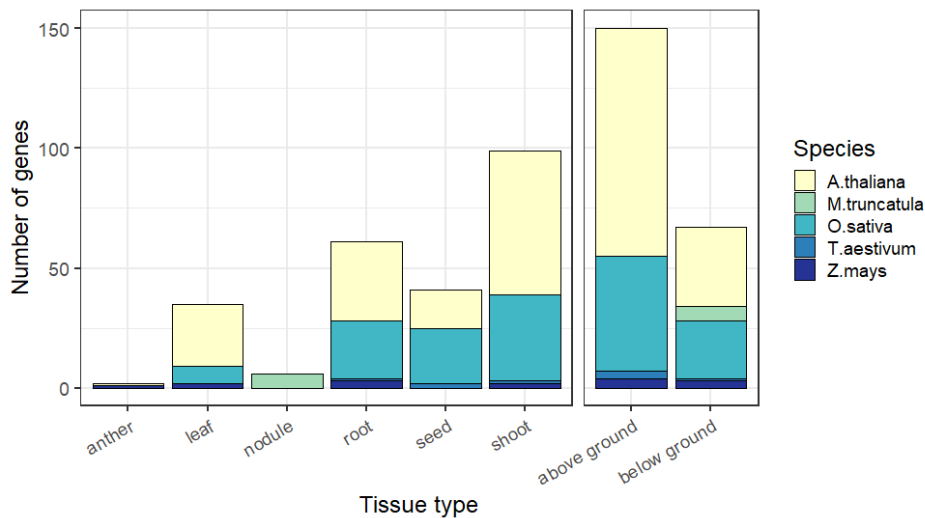




**Figure 2. Number of primary genes from each species listing each element.**

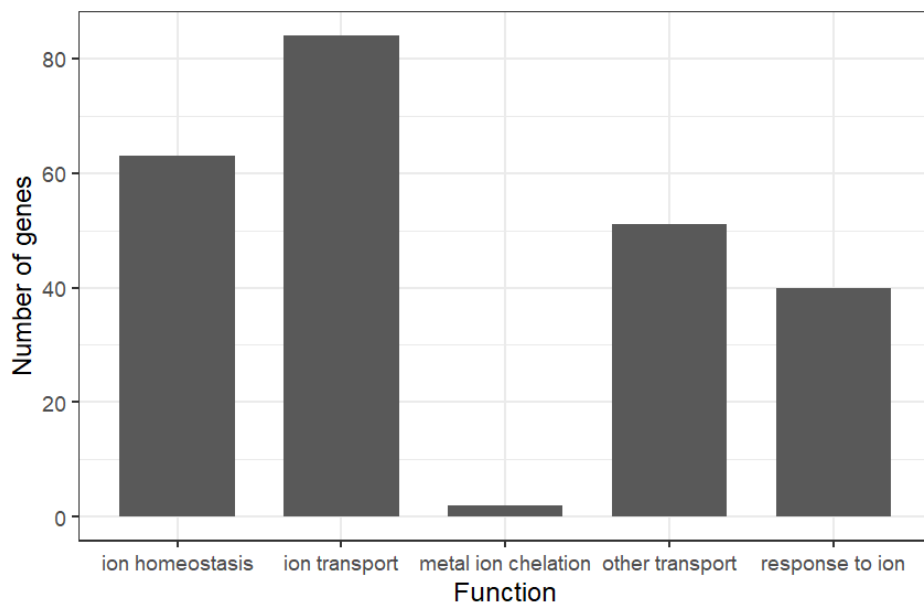
*A. thaliana* is the only species to have a primary gene listing for each element. There is a bias towards manganese, zinc and iron which have 2, 3 and 4 times more associated genes than the average  $13 \pm 12$  genes of other elements. Iron is the only element to contain genes from all five species in the primary list. In addition to biases 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.





**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. (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.



**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 [Prowler tool to search their biological processes terms](#) for the number of *A. thaliana* genes encoding predicted elemental transporters. We found [290](#) *A.thaliana* genes predicted to encode elemental transport, and only [16](#) 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, [245](#) of the genes from ThaleMine were not found in the [290](#) from PANTHER.

## 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 [65%](#) 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 [54](#) papers identifying primary genes in rice, [39](#) 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.

[While our list is focused on elements measured by ICP-MS, a known gene list for other elements and any other trait can be easily created with our pipeline at <https://github.com/baxterlab/KIG>. Our repository also contains user instructions on how to add more species from Phytozome to the list.](#)

### 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 STable1 ([xlsx](#)), and machine readable files (csv) can be found at <https://github.com/baxterlab/KIG>. Future updates to the list can be found at <https://docs.google.com/spreadsheets/d/1Xl2l1vtVJiHrIXLeOS5yTQQnLYq7BOHpmjuC-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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