## Supplementary Materials

### Table S1. Summary of the *lpa* mutants isolated in different species. nd, not determined; OE, overexpression; RNAi, RNA interference.

| Gene Function | Species       | Locus            | Origin of Mutation | Mutant (Ecotype) | Seed PA Reduction | Metabolites and/or Genes DOWN Regulated | Metabolites and/or Genes UP Regulated | Other Phenotypic Alterations | Ref. |
|---------------|---------------|------------------|--------------------|------------------|-------------------|----------------------------------------|---------------------------------------|-----------------------------------|------|
| MIPS1         | *Arabidopsis thaliana* | At4g39800       | T-DNA insertion | atips1-1 (Col), atips1-2 (Ws) | nd                | phytic acid, myo-inositol and galactinol in leaves |                                     | reduced cell proliferation in seedling causing strong modification of the root cap and shorter seedling; abnormal cotyledons; leaf lesions on adult plants modulated by light intensity and developmental stages, due to SA-dependent PCD (increase in SA content); increased resistance to oomycete | [1,2] |
| MIPS1         | *Arabidopsis thaliana* | At4g39800       | T-DNA insertion | mips1-2 (Col), mips1-4 (C-24), mips1-5 (Col) | nd                |                                     |                                     | defects in: embryogenesis, cotyledon vein patterning, epidermal cell division, root growth and gravitropism, root cap cell patterning, apical dominance, auxin response | [3]  |
| MIPS1         | *Arabidopsis thaliana* | At4g39800       | T-DNA insertion | mips1-2 (Col), mips1-3 (Col) | nd                | myo-inositol, ascorbic acid, phosphatidyl inositol, ceramides |                                     | smaller plants, curly leaves, spontaneous lesions, increased sensitivity to ABA and NaCl in germination | [4]  |
| MIPS2         | *Arabidopsis thaliana* | At2g22240       | T-DNA insertion | atips2 (Col) | none              | phytic acid in leaves |                                     | increased susceptibility to viruses, fungi, bacteria | [1,5,6] |
| MIPS3         | *Arabidopsis thaliana* | At5g10170       | T-DNA insertion | atips3 (Col) | none              |                                     | lethal                                 |                                     | [2,5,6] |
| MIPS1         | *Glycine max* | Glyma18g02210   | γ-rays             | Gm-lpa-TW75-1 | 50%               | myo-inositol, galactinol, raffinose, stachyose, galactopinitol A, galactopinitol B, fagopyritol B1, galactinol, sucrose, glycerol, sorbitol |                                     | reduced field emergence (seeds produced in subtropical environment) | [7–9] |
| MIPS1         | *Glycine max* | Glyma18g02210   | N-nitroso-N-methylurea | LR33 | 50%               | myo-inositol, raffinose, stachyose | sucrose | reduced field emergence (seeds produced in subtropical environment) | [10,11] |
Table S1. Cont.

| Gene Function | Species | Locus | Origin of Mutation | Mutant (Ecotype) | Seed PA Reduction | Metabolites and/or Genes DOWN Regulated | Metabolites and/or Genes UP Regulated | Other Phenotypic Alterations | Ref. |
|---------------|---------|-------|-------------------|------------------|------------------|----------------------------------------|--------------------------------------|----------------------------------|------|
| MIPS1         | Glycine max | Glyma18g02211 | V99-5089 | 50% | sucrase | Phytic acid in tubers, \(\text{myo-}
|               |         |       |                   |                  |                  | inositol (leaf and tuber), galactinol, raffinose (leaf), sucrase, starch (tuber) | | reduced apical dominance, delayed flowering, increased leaf thickness, precocious leaf senescence, mini tubers, no anthocyanins in tuber skin, increased susceptibility to virus | [12,13] |
| MIPS1         | Glycine max | Glyma18g02212 | RNAi ΔGmMIPS | 35%–95% | sucrase, starch (leaf) | | | | [14] |
| MIPS          | Solanum tuberosum | | antisense | antisense StIPS | nd | | | | [1,15] |
| MIPS          | Oryza sativa | Os03g09250 | antisense | antisense RINO1 under olesin 18kDa promoter (Ole18) | 75% | | | | [16] |
| IMP           | Arabidopsis thaliana | A3g02870 | T-DNA insertion | vtc4 | nd | myo-inositol, ascorbic acid | galactose | | [17] |
| IMT from M. crystallinum | Brassica napus | | over-expression | pNIMT (IMT under napin promoter) and pPhIMT (IMT under phaseolin promoter) | 20%–30% | galactinol, raffinose | galactose, stachyose, sucrose | | [18] |
| MIK           | Arabidopsis thaliana | At5g58730 | T-DNA insertion | atmk-1 | 62% | IPK2β, ITPK1, ITPK4, MRP, 2PGK | | reduced germination on NaCl, mannitol, \(\text{H}_{2}\text{O}_{2}\) | [5] |
| MIK           | Arabidopsis thaliana | At5g58730 | T-DNA insertion | atmk-2 | 66% | | | | [5] |
| MIK           | Zea mays | GRMZM2G361593 | Mu insertion | lpa3 | 45% | lower InsPs | myo-inositol | | [19] |
| MIK + ITPK    | Zea mays | GRMZM2G361593 | Mu insertion | lpa2-lpa3 | 66% | molar increase of lower InsPs | | | [19] |
| MIK           | Oryza sativa | Os03g52760 | γ-rays + sodium azide | Os-lpa-XS110-1 | 64% | InsP | myo-inositol, raffinose, galactose, galactinol, fructose, glucose | | | [20–23] |
| MIK           | Oryza sativa | EMS | lpa N15-186 | 75% | myo-inositol | | | | [24] |
| Gene Function | Species | Locus | Origin of Mutation | Mutant (Ecotype) | Seed PA Reduction | Metabolites and/or Genes DOWN Regulated | Metabolites and/or Genes UP Regulated | Other Phenotypic Alterations | Ref. |
|---------------|---------|-------|-------------------|-----------------|------------------|----------------------------------------|--------------------------------------|----------------------------------|-----|
| 2-PGK | Arabidopsis thaliana | At5g60760 | T-DNA insertion | Oslpa1 like | 66% | MIK, ITPK1, ITPK4, MRP | IPK2β, IPK1 | reduced germination on NaCl, mannitol, H₂O₂ | [25,5] |
| 2-PGK | Oryza sativa | Os02g57400 | γ-rays | XQZ-1 | 40% | molar increase of lower InsPs | | seed dry weight reduction, low grain yield, reduced germination (particularly after aging) | [22] |
| 2-PGK | Oryza sativa | Os02g57400 | γ-rays | KBNT lpa1-1 | 40% | molar increase of lower InsPs | | normal plants, reduced size of globoïds | [24] |
| IPK2β | Arabidopsis thaliana | At5g61760 | T-DNA insertion | ipk2β-1 | 35% | MIK, 2PGK | IPK1, MRP | reduced germination on NaCl, mannitol, H₂O₂ | [5] |
| IPK2β | Arabidopsis thaliana | At5g61760 | ipk2β-2 | | 48% | MIK, ITPK1, ITPK4, 2PGK | IPK1, MRP | reduced germination on NaCl, mannitol, H₂O₂ | [5] |
| ITPK1 | Arabidopsis thaliana | At5g16760 | T-DNA insertion | atitpk1 | 46% | MIK, 2PGK | IPK1, MRP | reduced germination on NaCl, mannitol, H₂O₂ | [5] |
| ITPK4 | Arabidopsis thaliana | At2g43980 | T-DNA insertion | atitpk4-1 | 51% | MIK, 2PGK | IPK1, MRP | reduced germination on NaCl, mannitol, H₂O₂ | [5] |
| ITPK4 | Arabidopsis thaliana | At2g43980 | T-DNA insertion | atitpk4-2 | 40% | | | | |
| ITPK | Zea mays | GRMZM2G456626 | Mu insertion | lpa2 | 30% | molar increase of lower InsPs | | seed dry weight reduction | [27,28] |
| ITPK | Oryza sativa | Os09g34300 | EMS | itpk | 46%–68% | | | seed dry weight reduction, low grain yield, reduced germination | [29] |
| IPK1 | Arabidopsis thaliana | At5g42810 | T-DNA insertion | ipk1-1 | 83% | | | altered Pi homeostasis (smaller leaves and epinasty at standard Pi concentration, longer roots at lower Pi concentration, attenuated ability to sense Pi increase) | [26] |
| IPK1 | Arabidopsis thaliana | At5g42810 | T-DNA insertion | ipk1-1 | 49% | MIK | IPK2β, ITPK1, ITPK4, MRP, 2PGK | reduced germination on NaCl, mannitol, H₂O₂ | [5] |
| IPK1 | Arabidopsis thaliana | At5g42810 | T-DNA insertion | ipk1-1 | nd | phytic acid in leaves | | increased susceptibility to viruses, fungi, bacteria | [1] |
### Table S1. Cont.

| Gene Function | Species         | Locus         | Origin of Mutation | Mutant (Ecotype) | Seed PA Reduction | Metabolites and/or Genes DOWN Regulated | Metabolites and/or Genes UP Regulated | Other Phenotypic Alterations                                                                 | Ref. |
|---------------|-----------------|---------------|--------------------|------------------|-------------------|----------------------------------------|---------------------------------------|---------------------------------------------------------------------------------------------|------|
| IPK1          | Arabidopsis thaliana | At5g42810     | T-DNA insertion    | ipk1-1           | nd                | increased Pi uptake and increased root to shoot translocation, Pi deficiency-like root system architecture |                                       | [30]                                                                                           |
| IPK1          | Arabidopsis thaliana | At5g42810     | T-DNA insertion    | ipk1-1           | nd                | early flowering, seed yield 52% of wt, reduced sensitivity to salt stress |                                       | [31]                                                                                           |
| IPK1          | Arabidopsis thaliana | At5g42810     | T-DNA insertion    | ipk1-2           | nd                | not viable                             |                                       | [30]                                                                                           |
| IPK1          | Glycine max     | Glyma14g07880 | γ-rays             | Gm-lpa-ZC-2-46%  |                   | myo-inositol, syringic acid, total isoflavones, molar increase of lower InsPs | shorter plants, but no yield reduction | [7]                                                                                             |
| IPK1          | Zea mays        | GRMZM2G067299 | ZFN-DNA editing    | ipk1-50%         |                   |                                         |                                       | [32]                                                                                           |
| IPK1          | Oryza sativa    | Os04g56580    | RNAi under Oleosin | ipk1-70%         |                   | unchanged levels of myo-inositol       |                                       | [33]                                                                                           |
| MRP           | Arabidopsis thaliana | At1g04120     | T-DNA insertion    | atmrp5-1 (Ws)    | nd                | on 0.5 × MS decreased root growth and increased lateral root formation, on 1 × MS reverse phenotype, increased level of auxin in root, no effect of sulfonylurea glibenclamide on stomatal opening |                                       | [34]                                                                                           |
| Gene Function | Species | Locus | Origin of Mutation | Mutant (Ecotype) | Seed PA Reduction | Metabolites and/or Genes DOWN Regulated | Metabolites and/or Genes UP Regulated | Other Phenotypic Alterations |
|---------------|---------|-------|--------------------|------------------|------------------|-----------------------------------------|-------------------------------------|----------------------------|
| MRP | Arabidopsis thaliana | At1g04120 | T-DNA insertion | atmrp5-1 (Ws) | nd | | | more resistant to drought stress, increased water use efficiency, stomata closer under light, no sensitivity to Ca2+ and ABA on stomatal closure, no sensitivity to auxin for opening under darkness, reduced ABA sensitivity during germination [35] |
| MRP | Arabidopsis thaliana | At1g04120 | T-DNA insertion | atmrp5-1 (Ws) | nd | | | impairment in activation of slow S-type anion channels in the plasma membrane of GCs [36] |
| MRP | Arabidopsis thaliana | At1g04120 | T-DNA insertion | atmrp5-2 (Ws) | nd | | | hypersensitivity to salt stress [37] |
| MRP | Arabidopsis thaliana | At1g04120 | T-DNA insertion | mpr5-1 (Ws), mpr5-2 (Col) | 73%–80% | 34%–37% reduction in total P, reduction in Na, Mg, Ca, K content | | reduced germination on NaCl, mannitol, H2O2 [5] |
| MRP | Arabidopsis thaliana | At1g04120 | T-DNA insertion | atmrp5-1 and 5-2 (Col) | 73%–80% | MIK, IPK2βITPK1, ITPK4, 2PGK | IPK1 | reduced germination on NaCl, mannitol, H2O2 [5] |
| MRP | Arabidopsis thaliana | At1g04120 | T-DNA insertion | atmrp5 (Col) | nd | | | enhanced lateral roots and root hair growth [30] |
| MRP | Arabidopsis thaliana | At1g04120 | T-DNA insertion | atmrp5 (Col) | nd | | | increase in InsP5, InsP7 and InsP8 in siliques [39] |
| MRP | Glycine max | Glyma03g32500, Glyma19g35230 | EMS | CX1834 | 80% | palmitate, stearate, oil | | reduced seedling and field emergence (seeds produced in subtropical environment) [12,13, 40–43] |
| MRP | Phaseolus vulgaris | Phvul001g165500 | EMS | lpa1 | 90% | myo-inositol, raffinosaccharides, MIPS, IMP, IPK2, ITPKα, IPK1 | | down-regulation of genes (MIPS, IMP, IPK2, ITPKα, IPK1) for PA biosynthetic pathway, germination hypersensitivity to ABA [44] |
| Gene Function | Species | Locus | Origin of Mutation | Mutant (Ecotype) | Seed PA Reduction | Metabolites and/or Genes DOWN Regulated | Metabolites and/or Genes UP Regulated | Other Phenotypic Alterations | Ref. |
|---------------|---------|-------|-------------------|------------------|-----------------|-----------------------------------------|--------------------------------|----------------------------------|------|
| MRP           | Zea mays | GRMZM5G820122 | EMS | lpa1-241, lpa1-7 | 90% | myo-inositol, MIPS | Mg, K | seed dry weight reduction, down-regulation of MIPS, altered morphology of globoids (number and size), altered embryo development, size, germination, seedling growth rate, ear size, increased susceptibility to oxidative stress | [45–50] |
| MRP           | Zea mays | GRMZM5G820123 | EMS | lpa1-1 | 66% | MIPS | myo-inositol | reduced germination, reduced vigour under stress conditions, altered morphology of globoids (number and size) | [27,32, 51–53] |
| MRP           | Oryza sativa | Os03g04920 | γ-rays + sodium azide | Os-lpa-XS110-2 | 20% | myo-inositol, raffinose, galactose | 24-methylencycloartanol (steroid) | seed dry weight reduction, low grain yield, reduced germination (particularly after aging), reduced field emergence. | [20–22, 54] |
| MRP           | Oryza sativa | Os03g04920 | γ-rays + sodium azide | Os-lpa-XS110-3 | 100% | myo-inositol | (lethal) | (lethal) | [20,54] |
| PAP           | Arabidopsis thaliana | At3g07130 | over-expression | OE-PAP15 | nd | phytic acid in leaves | ascorbic acid | altered salt, osmotic stress, and ABA sensitivities, enhanced salt tolerance, and decreased abscisic acid sensitivity | [55] |
| Sultr3;3      | Hordeum vulgare | sodium azide | lpa1-1 (M422) | 50% | IMP | Increase in free Pi and small increases in Ins(1,2,3,4,6)Py | reduced test weight and percentage plump kernels, mutation affects only aleurone. Breeding can abolish/reduce negative traits | [56–60] |
| Sultr3;3      | Oryza sativa | Os04g0652400 | γ-rays | MH86-1 | 44% | molar increase in free Pi | seed dry weight reduction, low grain yield, reduced germination (particularly after aging) | [20,22] |
| Gene Function | Species      | Locus          | Origin of Mutation | Mutant (Ecotype) | Seed PA Reduction | Metabolites and/or Genes DOWN Regulated | Metabolites and/or Genes UP Regulated | Other Phenotypic Alterations | Ref. |
|---------------|--------------|----------------|--------------------|------------------|------------------|-----------------------------------------|---------------------------------------|----------------------------------|------|
| unknown       | Pisum sativum| unknown        | EMS                | 1-150-81; 1-2347-144 | 60%–65%          | molar increase in free Pi                | decreased seed weight, decreased yield | [61,62]                         |      |
| unknown       | Hordeum vulgare | unknown        | sodium azide      | lpa3-3 (M635)    | 65%              | IMP, MIPS                               | myo-inositol, galactinol              | reduced test weight and percentage plump kernels, reduced yield. Breeding can abolish/reduce negative traits | [56–59] |
| unknown       | Hordeum vulgare | unknown        | sodium azide      | M955             | 90%              | IMP, MIPS                               | myo-inositol, raffinose, galactinol, sucrose | reduced test weight and percentage plump kernels, reduced yield. Breeding can abolish/reduce negative traits | [56,57, 59,63] |
| unknown       | Oryza sativa | unknown        | γ-rays            | Z9B-1            | 45%              | low increase in free Pi                 | seed dry weight reduction, low grain yield, reduced germination (particularly after aging) | [20,22]                         |      |
References

1. Murphy, A.; Otto, B.; Brearley, C.; Carr, J.; Hanke, D. A role for inositol hexakisphosphate in the maintenance of basal resistance to plant pathogens. Plant J. 2008, 56, 638–652.
2. Meng, P.; Raynaud, C.; Tcherkez, G.; Blanchet, S.; Massoud, K.; Domenichini, S.; Henry, Y.; Soubigou-Taconnat, L.; Lelarge-Trouverie, C.; Saindrenan, P.; et al. Crosstalks between myo-inositol metabolism, programmed cell death and basal immunity in Arabidopsis. PLoS ONE 2009, 4, doi:10.1371/journal.pone.0007364.
3. Chen, H.; Xiong, L. Myo-inositol-1-phosphate synthase is required for polar auxin transport and organ development. J. Biol. Chem. 2010, 285, 24238–24247.
4. Donahue, J.; Alford, S.; Torabinejad, J.; Kerwin, R.; Nourbakhsh, A.; Ray, W.; Hernick, M.; Huang, X.; Lyons, B.; Hein, P.; et al. The Arabidopsis thaliana myo-inositol 1-phosphate synthase1 gene is required for myo-inositol synthesis and suppression of cell death. Plant Cell 2010, 22, 888–903.
5. Kim, S.; Tai, T. Identification of genes necessary for wild-type levels of seed phytic acid in Arabidopsis thaliana using a reverse genetics approach. Mol. Genet. Genom. 2011, 286, 119–133.
6. Luo, Y.; Qin, G.; Zhang, J.; Liang, Y.; Song, Y.; Zhao, M.; Tsuge, T.; Aoyama, T.; Liu, J.; Gu, H.; et al. D-myo-inositol-3-phosphate affects phosphatidylinositol-mediated endomembrane function in Arabidopsis and is essential for auxin-regulated embryogenesis. Plant Cell 2011, 23, 1352–1372.
7. Yuan, F.; Zhao, H.; Ren, X.; Zhu, S.; Fu, X.; Shu, Q. Generation and characterization of two novel low phytate mutations in soybean (Glycine max L. Merr.). Theor. Appl. Genet. 2007, 115, 945–957.
8. Frank, T.; Nörenberg, S.; Engel, K.H. Metabolite profiling of two novel low phytic acid (lpa) soybean mutants. J. Agric. Food Chem. 2009, 57, 6408–6416.
9. Yuan, F.; Zhu, D.; Deng, B.; Fu, X.; Dong, D.; Zhu, S.; Li, B.; Shu, Q. Effects of two low phytic acid mutations on seed quality and nutritional traits in soybean (Glycine max L. Merr). J. Agric. Food Chem. 2009, 57, 3632–3638.
10. Hitz, W.; Carlson, T.; Kerr, P.; Sebastian, S. Biochemical and molecular characterization of a mutation that confers a decreased raffinosaccharide and phytic acid phenotype on soybean seeds. Plant Physiol. 2002, 128, 650–660.
11. Meis, S.; Fehr, W.; Schnebly, S. Seed source effect on field emergence of soybean lines with reduced phytate and raffinose saccharides. Crop Sci. 2003, 43, 1336–1339.
12. Maupin, L.; Rosso, M.; Rainey, K. Environmental effects on soybean with modified phosphorus and sugar composition. Crop Sci. 2011, 51, 642–650.
13. Gao, Y.; Biyashev, R.; Maroof, M.; Glover, N.; Tucker, D.; Buss, G. Validation of low-phytate qtls and evaluation of seedling emergence of low-phytate soybeans. Crop Sci. 2008, 48, 1355–1364.
14. Nunes, A.; Vianna, G.; Cuneo, F.; Amaya-Farfan, J.; de Capdeville, G.; Rech, E.; Aragao, F. RNAi-mediated silencing of the myo-inositol-1-phosphate synthase gene (GmMIPS1) in transgenic soybean inhibited seed development and reduced phytate content. Planta 2006, 224, 125–132.
15. Keller, R.; Brearley, C.; Trethewey, R.; Muller-Rober, B. Reduced inositol content and altered morphology in transgenic potato plants inhibited for 1D-myoinositol 3-phosphate synthase. Plant J. 1998, 16, 403–410.

16. Kuwano, M.; Mimura, T.; Takaiwa, F.; Yoshida, K. Generation of stable “low phytic acid” transgenic rice through antisense repression of the 1D-myoinositol 3-phosphate synthase gene (RINO1) using the 18-kDa oleosin promoter. Plant Biotechnol. J. 2009, 7, 96–105.

17. Torabinejad, J.; Donahue, J.; Gunasekera, B.; Allen-Daniels, M.; Gillaspy, G. VTC4 is a bifunctional enzyme that affects myo-inositol and ascorbate biosynthesis in plants. Plant Physiol. 2009, 150, 951–961.

18. Dong, J.; Yan, W.; Bock, C.; Nokhrina, K.; Keller, W.; Georges, F. Perturbing the metabolic dynamics of myo-inositol in developing brassica napus seeds through in vivo methylation impacts its utilization as phytate precursor and affects downstream metabolic pathways. BMC Plant Biol. 2013, 13, 84, doi:10.1186/1471-2229-13-84.

19. Shi, J.; Wang, H.; Hazebroek, J.; Ertl, D.; Harp, T. The maize low-phytic acid 3 encodes a myo-inositol kinase that plays a role in phytic acid biosynthesis in developing seeds. Plant J. 2005, 42, 708–719.

20. Liu, Q.; Xu, X.; Ren, X.; Fu, H.; Wu, D.; Shu, Q. Generation and characterization of low phytic acid germplasm in rice (Oryza sativa L.). Theor. Appl. Genet. 2007, 114, 803–814.

21. Frank, T.; Meuleye, B.; Miller, A.; Shu, Q.; Engel, K. Metabolite profiling of two low phytic acid (lpa) rice mutants. J. Agric. Food Chem. 2007, 55, 11011–11019.

22. Zhao, H.; Liu, Q.; Fu, H.; Xu, X.; Wu, D.; Shu, Q. Effect of non-lethal low phytic acid mutations on grain yield and seed viability in rice. Field Crop. Res. 2008, 108, 206–211.

23. Emami, K.; Morris, N.J.; Cockell, S.J.; Golebiowska, G.; Shu, Q.Y.; Gatehouse, A.M. Changes in protein expression profiles between a low phytic acid rice (Oryza sativa L. Ssp. Japonica) line and its parental line: A proteomic and bioinformatic approach. J. Agric. Food Chem. 2010, 58, 6912–6922.

24. Kim, S.; Andaya, C.; Newman, J.; Goyal, S.; Tai, T. Isolation and characterization of a low phytic acid rice mutant reveals a mutation in the rice orthologue of maize MIK. Theor. Appl. Genet. 2008, 117, 1291–1301.

25. Kim, S.; Tai, T. Genetic analysis of two OsLpa1-like genes in Arabidopsis reveals that only one is required for wild-type seed phytic acid levels. Planta 2010, 232, 1241–1250.

26. Stevenson-Paulik, J.; Bastidas, R.; Chiou, S.; Frye, R.; York, J. Generation of phytate-free seeds in Arabidopsis through disruption of inositol polyphosphate kinases. Proc. Natl. Acad. Sci. USA 2005, 102, 12612–12617.

27. Raboy, V.; Gerbasi, P.; Young, K.; Stoneberg, S.; Pickett, S.; Bauman, A.; Murthy, P.; Sheridan, W.; Ertl, D. Origin and seed phenotype of maize low phytic acid 1-1 and low phytic acid 2-1. Plant Physiol. 2000, 124, 355–368.

28. Shi, J.; Wang, H.; Wu, Y.; Hazebroek, J.; Meeley, R.; Ertl, D. The maize low-phytic acid mutant lpa2 is caused by mutation in an inositol phosphate kinase gene. Plant Physiol. 2003, 131, 507–515.

29. Kim, S.; Tai, T. Identification of novel rice low phytic acid mutations via TILLING by sequencing. Mol. Breed. 2014, 34, 1717–1729.
30. Kuo, H.; Chang, T.; Chiang, S.; Wang, W.; Ching, Y.; Chiou, T. *Arabidopsis* inositol pentakisphosphate 2-kinase, AtIPK1, is required for growth and modulates phosphate homeostasis at the transcriptional level. *Plant J.* 2014, 80, 503–515.

31. Lee, H.; Lee, D.; Cho, H.; Kim, S.; Auh, J.; Pai, H. InsP_6-sensitive variants of the Gle1 mRNA export factor rescue growth and fertility defects of the ipk1 low-phytic-acid mutation in *Arabidopsis*. *Plant Cell* 2015, 27, 417–431.

32. Shukla, S.; VanToai, T.; Pratt, R. Expression and nucleotide sequence of an ins (3) p-1 synthase gene associated with low-phytate kernels in maize (*Zea mays* L.). *J. Agric. Food Chem.* 2004, 52, 4565–4570.

33. Ali, N.; Paul, S.; Gayen, D.; Sarkar, S.; Datta, K.; Datta, S. Development of low phytate rice by rna mediated seed-specific silencing of inositol 1,3,4,5,6-pentakisphosphate 2-kinase gene (*IPK1*). *PLoS ONE* 2013, 8, doi:10.1371/journal.pone.0068161.

34. Gaedeke, N.; Klein, M.; Kolukisaoglu, U.; Forestier, C.; Muller, A.; Ansorge, M.; Becker, D.; Mannun, Y.; Kuchler, K.; Schulz, B.; *et al*. The *Arabidopsis thaliana* ABC transporter AtMRP5 controls root development and stomata movement. *EMBO J.* 2001, 20, 1875–1887.

35. Klein, M.; Perfus-Barbeoch, L.; Frelet, A.; Gaedeke, N.; Reinhardt, D.; Mueller-Roeber, B.; Martinoia, E.; Forestier, C. The plant multidrug resistance ABC transporter AtMRP5 is involved in guard cell hormonal signalling and water use. *Plant J.* 2003, 33, 119–129.

36. Suh, S.J.; Wang, Y.F.; Frelet, A.; Leonhardt, N.; Klein, M.; Forestier, C.; Mueller-Roeber, B.; Cho, M.H.; Martinoia, E.; Schroeder, J.I. The ATP binding cassette transporter AtMRP5 modulates anion and calcium channel activities in *Arabidopsis* guard cells. *J. Biol. Chem.* 2007, 282, 1916–1924.

37. Lee, E.; Kwon, M.; Ko, J.; Yi, H.; Hwang, M.; Chang, S.; Cho, M. Binding of sulfonylurea by AtMRP5, an *Arabidopsis* multidrug resistance-related protein that functions in salt tolerance. *Plant Physiol.* 2004, 134, 528–538.

38. Nagy, R.; Grob, H.; Weder, B.; Green, P.; Klein, M.; Frelet-Barrand, A.; Schjoerring, J.; Brearley, C.; Martinoia, E. The *Arabidopsis* ATP-binding cassette protein AtMRP5/AtABCC5 is a high affinity inositol hexakisphosphate transporter involved in guard cell signaling and phytate storage. *J. Biol. Chem.* 2009, 284, 33614–33622.

39. Steger, D.; Haswell, E.; Miller, A.; Wente, S.; O’Shea, E. Regulation of chromatin remodeling by inositol polyphosphates. *Science* 2003, 299, 114–116.

40. Wilcox, J.; Premachandra, G.; Young, K.; Raboy, V. Isolation of high seed inorganic P, low-phytate soybean mutants. *Crop Sci.* 2000, 40, 1601–1605.

41. Oltmans, S.; Fehr, W.; Welke, G.; Raboy, V.; Peterson, K. Agronomic and seed traits of soybean lines with low-phytate phosphorus. *Crop Sci.* 2005, 45, 593–598.

42. Hulke, B.; Fehr, W.; Welke, G. Agronomic and seed characteristics of soybean with reduced phytate and palmitate. *Crop Sci.* 2004, 44, 2027–2031.

43. Pilu, R.; Panzeri, D.; Cassani, E.; Cerino Badone, F.; Landoni, M.; Nielsen, E. A paramutation phenomenon is involved in the genetics of maize low phytic acid1-241 (*lpa1-241*) trait. *Heredity* 2009, 102, 236–245.

44. Panzeri, D.; Cassani, E.; Doria, E.; Tagliabue, G.; Forti, L.; Campion, B.; Bollini, R.; Brearley, C.A.; Pilu, R.; Nielsen, E.; *et al*. A defective ABC transporter of the MRP family, responsible for the
bean lpa1 mutation, affects the regulation of the phytic acid pathway, reduces seed myo-inositol and alters aba sensitivity. New Phytol. 2011, 191, 70–83.

45. Pilu, R.; Panzeri, D.; Gavazzi, G.; Rasmussen, S.; Consonni, G.; Nielsen, E. Phenotypic, genetic and molecular characterization of a maize low phytic acid mutant (lpa241). Theor. Appl. Genet. 2003, 107, 980–987.

46. Pilu, R.; Landoni, M.; Cassani, E.; Doria, E.; Nielsen, E. The maize lpa241 mutation causes a remarkable variability of expression and some pleiotropic effects. Crop Sci. 2005, 45, 2096–2105.

47. Cerino Badone, F.; Amelotti, M.; Cassani, E.; Pilu, R. Study of low phytic acid1-7 (lpa1-7), a new ZmMRP4 mutation in maize. J. Hered. 2012, 103, 598–605.

48. Doria, E.; Galleschi, L.; Calucci, L.; Pinzino, C.; Pilu, R.; Cassani, E.; Nielsen, E. Phytic acid prevents oxidative stress in seeds: Evidence from a maize (Zea mays L.) low phytic acid mutant. J. Exp. Bot. 2009, 60, 967–978.

49. Cerino Badone, F.; Cassani, E.; Landoni, M.; Doria, E.; Panzeri, D.; Lago, C.; Mesiti, F.; Nielsen, E.; Pilu, R. The low phytic acid1-241 (lpa1-241) maize mutation alters the accumulation of anthocyanin pigment in the kernel. Planta 2010, 231, 1189–1199.

50. Landoni, M.; Cerino Badone, F.; Haman, N.; Schiraldi, A.; Fessas, D.; Cesari, V.; Toschi, I.; Cremona, R.; Delogu, C.; Villa, D.; et al. Low phytic acid 1 mutation in maize modifies density, starch properties, cations, and fiber contents in the seed. J. Agric. Food Chem. 2013, 61, 4622–4630.

51. Shi, J.; Wang, H.; Schellin, K.; Li, B.; Faller, M.; Stoop, J.; Meeley, R.; Ertl, D.; Ranch, J.; Glassman, K. Embryo-specific silencing of a transporter reduces phytic acid content of maize and soybean seeds. Nat. Biotech. 2007, 25, 930–937.

52. Liu, Z.; Cheng, F.; Cheng, W.; Zhang, G. Positional variations in phytic acid and protein content within a panicle of japonica rice. J. Cereal Sci. 2005, 41, 297–303.

53. Naidoo, R.; Tongoona, P.; Derera, J.; Laing, M.; Watson, G. Combining ability of low phytic acid (lpa-1) and quality protein maize (qpm) lines for seed germination and vigour under stress and non-stress conditions. Euphytica 2012, 185, 529–541.

54. Xu, X.; Zhao, H.; Liu, Q.; Frank, T.; Engel, K.; An, G.; Shu, Q. Mutations of the multi-drug resistance-associated protein ABC transporter gene 5 result in reduction of phytic acid in rice seeds. Theor. Appl. Genet. 2009, 119, 75–83.

55. Zhang, W.; Gruszewski, H.; Chevone, B.; Nessler, C. An arabidopsis purple acid phosphatase with phytase activity increases foliar ascorbate. Plant Physiol. 2008, 146, 431–440.

56. Bregitzer, P.; Raboy, V. Effects of four independent low-phytate mutations on barley agronomic performance. Crop Sci. 2006, 46, 1318–1322.

57. Raboy, V.; Peterson, K.; Jackson, C.; Marshall, J.; Hu, G.; Saneoka, H.; Bregitzer, P. A substantial fraction of barley (Hordeum vulgare L.) low phytic acid mutations have little or no effect on yield across diverse production environments. Plants 2015, 4, 225–239.

58. Karner, U.; Peterbauer, T.; Raboy, V.; Jones, D.; Hedley, C.; Richter, A. Myo-inositol and sucrose concentrations affect the accumulation of raffinose family oligosaccharides in seeds. J. Exp. Bot. 2004, 55, 1981–1987.

59. Dorsch, J.; Cook, A.; Young, K.; Anderson, J.; Bauman, A.; Volkmann, C.; Murthy, P.; Raboy, V. Seed phosphorus and inositol phosphate phenotype of barley low phytic acid genotypes. Phytochemistry 2003, 62, 691–706.
60. Ye, H.; Zhang, X.; Broughton, S.; Westcott, S.; Wu, D.; Lance, R.; Li, C. A nonsense mutation in a putative sulphate transporter gene results in low phytic acid in barley. *Funct. Integr. Genom.* 2011, 11, 103–110.

61. Rehman, A.; Shunmugam, A.; Arganosa, G.; Bett, K.; Warkentin, T. Inheritance of the low-phytate trait in pea. *Crop Sci.* 2012, 52, 1171–1175.

62. Shunmugam, A.S.K.; Bock, C.; Arganosa, G.C.; Georges, F.; Gray, G.R. and Warkentin, T.D. Accumulation of phosphorus-containing compounds in developing seeds of low-phytate pea (*Pisum sativum* L.) mutants. *Plants* 2015, 4, 1–26.

63. Raboy, V. *Myo*-inositol-1,2,3,4,5,6-hexakisphosphate. *Phytochemistry* 2003, 64, 1033–1043.

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