Phosphorus Transport in Arabidopsis and Wheat: Emerging Strategies to Improve P Pool in Seeds

Mushtak Kisko [1] [iD]**, Vishnu Shukla** [2]**, Mandeep Kaur** [2]**, Nadia Bouain** [1]**, Nanthana Chaiwong** [1]**, Benoit Lacombe** [1]**, Ajay Kumar Pandey** [2] **and Hatem Rouached** [1],*,[†] [iD]

1. BPMP, Univ Montpellier, CNRS, INRA, SupAgro, 34060 Montpellier, France; mushtakkisko@gmail.com (M.K.); nadia.bouain@gmail.com (N.B.); nantana.c189@gmail.com (N.C.); benoit.lacombe@supagro.fr (B.L.)
2. Department of Biotechnology, National Agri-Food Biotechnology Institute, Sector 81, S.A.S. Nagar (Mohali), Punjab 140306, India; shuklavrk@gmail.com (V.S.); mandeep@nabi.res.in (M.K.); pandeyak1974@gmail.com (A.K.P.)
* Correspondence: hatem.rouached@inra.fr; Tel.: +33-(0)-4-99-61-31-54; Fax: +33-(0)-4-67-52-57-37
† Present Address: Department of Plant Biology, Carnegie Institution for Science, Stanford, CA 94305, USA.

Abstract: Phosphorus (P) is an essential macronutrient for plants to complete their life cycle. P taken up from the soil by the roots is transported to the rest of the plant and ultimately stored in seeds. This stored P is used during germination to sustain the nutritional demands of the growing seedling in the absence of a developed root system. Nevertheless, P deficiency, an increasing global issue, greatly decreases the vigour of afflicted seeds. To combat P deficiency, current crop production methods rely on heavy P fertilizer application, an unsustainable practice in light of a speculated decrease in worldwide P stocks. Therefore, the overall goal in optimizing P usage for agricultural purposes is both to decrease our dependency on P fertilizers and enhance the P-use efficiency in plants. Achieving this goal requires a robust understanding of how plants regulate inorganic phosphate (Pi) transport, during vegetative growth as well as the reproductive stages of development. In this short review, we present the current knowledge on Pi transport in the model plant *Arabidopsis thaliana* and apply the information towards the economically important cereal crop wheat. We highlight the importance of developing our knowledge on the regulation of these plants' P transport systems and P accumulation in seeds due to its involvement in maintaining their vigour and nutritional quality. We additionally discuss further discoveries in the subjects this review discusses substantiate this importance in their practical applications for practical food security and geopolitical applications.

Keywords: phosphate; seeds; Arabidopsis; wheat

1. Introduction

Phosphorus (P) is an essential macronutrient for plant growth and production [1,2]. P deficiency is a generally widespread stressor occurring in natural and agricultural environments. Consequently, global agricultural crop production has been severely affected [2,3]. It is estimated that crop yield on 30–40% of the world's total arable land is limited by inorganic phosphate (Pi) bioavailability [4,5]. Many causes could explain the low availability of Pi to plants, such as the Pi (HPO_4^{2-}) interaction with soil cations such as zinc (Zn^{2+}) or iron (Fe^{2+}), which form an insoluble complex [6–8]. In addition, and most importantly, global Pi reserves are rapidly decreasing due to an increase in its demand [2,9–11]. Analysis of data collected over 14 years revealed that the usage of global P fertilizer considerably increased at a rate of about 357,000 t/annum (i.e., an annual increase of 2.4%) [12,13]. Experts agree that the world is facing serious P crisis [14,15] and that the global P reserve is not distributed uniformly [5]. Taken together, these issues constitute compelling evidence justifying a direct link

between Pi availability and the overwhelming world food security in coming few years. Developing a better understanding of how plants regulate Pi uptake for transport to different organs and seeds will help design new strategies to increase crop yield and simultaneously reduce P input.

Approximately 75% of Pi taken up by plant roots for use by vegetative tissues and vital storage in developing seeds is stored in the form of phytic acid (PA) [3]. Although P fertilizer supply has increased the yield of cereal grains such as wheat, a recent analysis showed that about 37% of wheat areas worldwide have experienced yield stagnation [16], highlighting the importance of precise management of P fertilizer application to achieve high wheat yield and quality. Achieving this objective necessitates a better understanding of how crops regulate P homeostasis. During the last decades, our knowledge on the molecular regulation of P transport and P redistribution in different plant organs during vegetative phase has progressed mainly in model plants such as *Arabidopsis thaliana* (for review, [17]). However, limited progress was achieved in crops such as wheat, a major dietary source of calories and protein for humans. In this short review, we present the recent progress of our understanding on Pi transport in wheat through information obtained for *A. thaliana*. We next highlight the importance of the knowledge generated on the molecular mechanisms which regulate the Pi transport and its accumulation in grains.

2. Phosphate Uptake and Transport in Wheat and Arabidopsis

In plants, Pi deficiency affects growth that manifests itself at a phenotypic level by affecting the aboveground and underground biomass. The effects of Pi availability on wheat growth is presented in Figure 1.

Figure 1. Changes in wheat growth under different phosphate conditions. (**A**) Wheat were grown hydroponically for three weeks in presence (+P) or absence (−P) of inorganic phosphate (KH_2PO_4). (**B**) shoot and (**C**) root of wheat grown either in presence (0.5 mM) or in absence of inorganic phosphate for three weeks.

Pi is acquired by root systems, which undergo a significant architectural change in response to Pi deficiency (for review, [18]) that is associated with increasing Pi uptake capacity through an upregulation of regulators and transporters involved in P-homeostasis [19]. To improve P use efficiency in crop plants, it is therefore prerequisite to understand P distribution within the plant.

Numerous Pi transporters have been identified in wheat [20–22] Gradual elucidation of these components and their roles have been effectively achieved through experiments either increasing P remobilization from senescing tissue or reducing the partition of P to developing grains [23]. However, initial identification of these transporters were generated from data collected for those of the model plant Arabidopsis [24]. In this dicot model plant, Pi transporters generally belong to a gene family referred to as phosphate transporter (*PHT*) [25]. The PHT family is divided into five

groups (*PHT1*, *PHT2*, *PHT3*, *PHT4*, and *PHT5*) differentiated primarily by their sub-cellular localization and functional properties. Plasma membrane-bound proteins belonging to the *PHT1* subfamily are primarily responsible for Pi uptake in Arabidopsis [25]. In contrast, PHT2 proteins are localized in chloroplasts, while PHT3/MPT proteins are mostly mitochondrial membrane transporters and *PHT4* proteins are Golgi-apparatus located transporters. A vacuolar Pi transporter was identified in Arabidopsis and designated as PHT5/VPT/SPX-MFS proteins [26].

Pi is also transported outside the root cells for distribution between different plant organs. The Phosphate 1 (*PHO1*) gene family contains 11 Pi exporter proteins mostly involved in the translocation of Pi from roots to shoots [27,28]. Among these molecular players, the mutation of both *PHT1;1* and *PHT1;4* or *PHO1* and *PHO1;H1* causes the most severe phenotype that is characterized by a decreased Pi accumulation in Arabidopsis [19,28], demonstrating the importance of these Pi transporters and exporters in Pi uptake and Pi translocation to shoots. For more information, readers are referred to these reviews [25,29].

The identification of Arabidopsis proteins involved in Pi distribution accelerated the discovery of wheat Pi transporters by exploring regions of the wheat genome with similar sequence to the genomic sequences of these Arabidopsis Pi transporters [20]. Validation and characterization of identified wheat Pi transporter candidates have been attained through evaluation of their genetic function either in Arabidopsis or by means of complementation with yeast mutants defective in Pi transport [30,31]. A cumulative list of members of the crop origin Pi-transporters is summarized in Table 1.

Table 1. Inventory for the list of genes and regulators those are involved in sensing, uptake and signaling during Pi limiting conditions in model plant Arabidopsis and *Triticum aestivum*.

Components of Phosphate Transport	*Arabidopsis thaliana*	*Triticum aestivum*
Sensing	*AtSIZ1* ([32])	NA*
	AtSPX1, AtSPX2, AtSPX3 & AtSPX4 ([33,34])	*TaSPX1* ([35])
	AtIPK1 ([36])	*TaIPK1* ([37])
Uptake & Transport	*AtPHT1;1–AtPHT1;9* ([38])	*TaPHT1.1-TaPHT1.13* ([20–22,39])
	AtPHT2;1 ([40])	*TaPHT2.1* ([41])
	AtPHT3;1–AtPHT3.3 ([42,43])	*TaPHT3.1–TaPHT3.3* ([20,44])
	AtPHT4;1–AtPHT4;6 ([45])	*TaPHT4.1–TaPHT4.6* ([20])
	AtPHT5;1–AtPHT5;3 ([46])	NA
	AtPHO1 ([27])	*TaPHO1* ([47])
Signaling	*AtPHR1* ([48])	*TaPHR1* ([49])
	AtPHL1 ([50])	NA
	AtPHF1 ([51])	NA
	AtPHO1 ([52])	NA
	AtPHO2 ([53])	*TaPHO2* ([47])
	AtZAT6 ([54])	NA
	AtARP6 ([55])	NA
	AtH2A.Z ([55])	NA
	AtWRKY6 ([56])	NA
	AtWRKY42 ([57])	NA
	AtWRKY45 ([58])	NA
	AtWRKY75 ([59])	NA
	AtNLA ([60])	NA
	AtIPS1 ([61])	*TaIPS1* ([44])
	AtmiR399 ([62])	*Tae-miR399-A1* ([47])
	AtMiR827 ([63])	NA
	AtALIX ([64])	NA

* NA: Not applicable.

The wheat genome contains several TaPHT members that could be divided into four subfamilies, PHT1 (*TaPHT1.1–1.13*), PHT2 (*TaPHT2.1*), PHT3 (*TaPHT3.1–3.3*), and PHT4 (*TaPHT4.1–4.6*). Their transcripts demonstrate enhanced expression in Pi limited roots and shoots ([20]). The complexity in discerning a total number of TaPHT1 members within the wheat genome has been recently discussed ([21]) while experiments characterizing the role of specific members involved in P uptake within two wheat genotypes (*KN9204* and *SJZ8*) have been performed. Differential expression pattern of high-affinity *TaPHTs* was observed in different wheat varieties under varying Pi regimes ([39]). Interestingly, the expression of *TaPHT1.1*, *1.2*, *1.9*, and *1.10* at flowering positively correlated with P uptake after stem elongation in different wheat varieties under field conditions supplemented with different P rates ([21]). Under Pi deprivation, Pi uptake increases and involves a high-affinity PHT1 member *TaPT2* ([65]). Down-regulation of *TaPHT2.1* was able to induce a pronounced decrease in Pi accumulation in both sufficient and Pi-deficient wheat, suggesting its association with other PHTs involved in Pi uptake and translocation within plants ([41]). This reinforces the impact the intracellular Pi transport mechanism has upon regulating the plant Pi uptake efficiency. Still, in contrast to the data known about Arabidopsis, little is known about the regulation of wheat Pi transporters at the protein levels ([66]). It is worth to note that apart from its role in Pi uptake, *TaPHT2.1* was functionally characterized as an important P signalling component involved in Pi translocation from cytosol to chloroplast in Pi-stressed leaves ([41]). Whether any Pi transporter in wheat could play an additional transceptor role remains an open question. Membrane proteins that fulfil a dual nutrient transport function, such as the *PHO1* ([67]) or nitrogen transporter *NRT1* ([68]), serve as extant examples. Other than *PHT2* members and some reports showing differential expression of *TaPHT3* and four transcript abundance under Pi-depleted roots and shoots ([20,44]), there is no detail on their precise biological role in wheat tissues/cell. In addition, recent expression profiles of wheat *PHT1* sub-family genes during hydroponic and field-grown plant tissues were correlated with the presence of cis-acting promoter elements ([22]). These studies showed growing interests in the crop Pi-transporters among researchers.

3. Phosphate Sensing and Signalling in Arabidopsis and Wheat

How plants sense and signal Pi deficiency has been a long-standing question. In Arabidopsis, decades of research eventually identified the Pi starvation signalling pathway, defined as *SPX1-PHR1-miR399-PHO2-PHT1/PHO1* (for review: [29,69]). Key genes encoding for SPX proteins was initially reported to be upregulated in response to P deficiency via transcriptome analysis ([70]). *SPX* genes perform diverse functions in plant tolerance to Pi starvation ([33]) and play an important role in sensing P concentration in the cytosol through its ability to bind the inositol polyphosphate signalling molecule ([71]). *SPX1* interacts with the transcription factor Phosphate Response 1 (*PHR1*) in presence of Pi and dissociates under Pi deficiency ([71]). *PHR1* regulates many Pi-related genes ([50]), such as the *miRNA399* that eventually targets Phosphate 2 (PHO2) transcripts. The reduction of PHO2 protein abundance leads to the accumulation of PHT1 and PHO1 proteins ([72]) and consequently an increase of the plant capacity to uptake Pi and translocate Pi to shoots ([73]). Noteworthy, the proper functioning of this signalling pathway requires the contribution of many others genes such the *SUMO E3 ligase SIZ1* ([32]), *PHOSPHATE TRANSPORTER TRAFFIC FACILITATOR1* (*PHF1*), ([51]) and *NITROGEN LIMITATION ADAPTATION* (NLA), ([60]). *SIZ1* is involved in the regulation of *PHR1* by sumoylation ([32]). *PHF1* is required for the trafficking of Pi transporters to the plasma membrane [51]. *NLA* is proposed to function at the plasma membrane to direct the degradation of *PHT1s* ([60]), a fine-tuning process required for Pi uptake capacity of plants.

In wheat, transcript profiles of genes involved in Pi starvation response with organ-specific Pi allocation patterns were studied in roots and shoots of Chinese 80–55 (P-efficient cultivar) and Machete (less-efficient cultivar) under Pi deficiency [44]. This report revealed the distinct modes for allocation of Pi and organic P compounds between the source and sink tissues that modulate the adaptation under varying Pi condition. The P-allocation patterns in the multiple plant organs correlated with

the transcript expression patterns, suggestive of molecular signatures for improved phosphorus use efficiency (PUE) during limited Pi supply. Few genes involved in Pi starvation signalling responses have been reported for hexaploid wheat [35], such as an ortholog of the Arabidopsis transcription factor PHR1 characterized for its function in regulating Pi-signalling and plant growth in wheat [49]. Under both Pi-sufficient and deficient conditions, over-expression of the *TaPHR1-A1* homolog moderately up-regulated the expression levels of *TaPHR1* throughout the plant, resulting in a moderate increase of leaf Pi concentration and thus avoiding resultant toxicity ([49]). Pi uptake was positively favoured by *TaPHR1-A1* over-expression by increasing root tip number, lateral root length, and *TaPHTs* expression (*TaPHT1.2* in roots and *TaPHT1.6* in shoots). Utilizing bimolecular fluorescence complementation assays, it has been confirmed that wheat PHR1 forms a homodimer and confers transcriptional activation of a putative downstream target Pi-transporter *TaPHT1.2* [49].

The presence of Arabidopsis PHO2 orthologs in hexaploid wheat has also been proposed [35]. Detailed analysis of respective mutant lines for three *TaPHO2* genes from homologous group1 (*A1*, *B1*, and *D1*) showed remarkably different effects on P uptake, distribution, and plant growth [47]. The overall expression of *TaPHO2* in wheat was severely reduced in a *tapho2-d1* mutant, leading to high total shoot P under limited Pi conditions, but also showed inhibited growth and yield [47]. This resembled the phenotype observed in a *pho2* mutant of both monocots (e.g., rice) and dicots (e.g., Arabidopsis) [74,75]. Interestingly, *tapho2-a1* knockout mutant plants showed reduced *TaPHO2* expression that leads to only a moderate increase of total P and Pi levels in leaf under both sufficient and deficient P conditions [47]. Unlike the *tapho2-d1* mutant, *tapho2-a1* mutants demonstrated a moderate increase in P levels and accumulation alongside improved plant growth and grain yield [47]. In light of these interesting data, the involvement of *TaPHO2-D1* in Pi homeostasis to maintain plant growth rather than a simple Pi starvation signalling pathway has been proposed [47]. The Pi starvation signalling pathway *PHR1-IPS1-miR399-UBC24/PHO2-PHT1/PHO1* seems to be conserved and functional in numerous plant species. Manipulating the components of this pathway could be an important strategy for improving Pi nutrition in crops.

These genes and molecular mechanisms involved in Pi stress response are specifically induced during Pi deficiency and not under any other modes of stress known to alter Pi homeostasis. These observations indicate the existence of additional unknown genes and pathways regulating the Pi content in plants [8,52]. For instance, it is now well established that Pi content in plants is altered when plants are challenged by zinc limitation (−Zn) [6,76–79]. Intriguingly, under single −Zn stress, an excess of Pi supply causes loss of wheat biomass in comparison with plants grown under –P-Zn simultaneous stress [78]. Nevertheless, despite its fundamental importance, very little is known about the regulatory network established during Zn deficiency to control Pi homeostasis [52]. Studying Zn/Pi homeostasis interactions will lead us to uncover new genes and pathways controlling plant Pi homeostasis. This knowledge will be an additional resource for the improving Pi usage through perturbing Zn deficiency signalling pathways.

These experiments have all begun to clarify the components and systems that regulate P/Pi sensing and signalling within plants. The emergence of genome editing tools holds promise for further studies perturbing specific Pi-related genes/pathways, or genes involved in modulating the Pi content, such as genes involved in Zn deficiency signalling, to ultimately improve Pi nutrition in crops [80].

4. Phosphate in Seeds

The accumulation of nutrients in the seed is important for seed vigour and germination [81]. The amount of micronutrients in seeds has declined systematically since the beginning of the green revolution in the 1960s [82,83]. In contrast, phytic acid (PA), the organic form of P in seeds, has increased following global changes (e.g., elevated atmospheric CO_2) in various plant species including wheat [84]. Since PA is considered an anti-nutrient, increasing Pi content in grain while decreasing PA has become a trait of great interest [85].

In general, while Pi uptake and its intracellular and long-distance transport in plants has been extensively studied, the Pi transport in seeds has received little attention [86]. Current knowledge on the role of seed-specific PHTs is largely lacking [87]. In the seeds, nutrients reach the embryo via various pathways and at different developmental stages. Transfer of nutrients from the maternal seed coat to the filial endosperm and embryo is required for seed production and quality. In the case of Pi, the transfer of this element from the seed coat to the embryo requires Pi exporters. Recently, the *PHO1* gene was shown to be expressed in the chalazal seed coat in Arabidopsis, suggesting a role in the transfer of P from the seed coat to the embryo in developing seeds [88]. Consistently, Pi transfer from the seed coat to the embryo is perturbed in the *pho1* mutant. This observation and experimental data state the ignition point for a deep investigation of Pi transport in seeds, which may help to start understanding the mechanism regulating P accumulation.

In wheat, the mature grain may contain up to 90% of the total shoot P, with 20–90% of this being translocated from other tissues (for details, see [89]). PA accounts for up to 1–2% of the total weight [90,91]. P and PA concentrations in the grain increases as P application increases [92]. Increased PA concentration greatly decreases the bioavailability of nutritional minerals in wheat grain, such as Zn [92]. Therefore, reduction of PA in cereal grains is considered an important trait that is generated either through breeding or biotechnological approaches. Reducing PA in grains may provide a dual gain with less grain P loss and more micronutrient retention [93,94]. Generation of low PA crops may be achieved by targeting PA biosynthesis genes or transport [29,95–98]. As an alternative strategy to achieve low PA grains, roles for other families of transporters are also emerging. For instance, knockdown of the rice Pi transporter *OsPHT1.8* resulted in lowered PA accumulation in the embryo and mature grains [94]. Subsequently, they showed that rice *PHT1.8* performs a novel biological function during crosstalk between Pi and auxin signalling. This was one of the recent reports that provided clues for the link between auxin and -Pi responses [99]. Sulphate transporters have also implicated in grain PA and P content regulation. Map-based cloning and complementation tools resulted in the identification of rice sulphate transporters referred as *OsSULTR3;3*, which are involved in compositional changes of Pi and PA in developing grains [100]. Subsequently, another sulphate transporter family gene named the *SULTR-like phosphorus distribution transporter* (*SPDT*) has demonstrated involvement in the intervascular transfer of P, especially at the nodes by unloading P from xylem toward the phloem [101]. Therefore, such studies have suggested that node-localized transporters could affect the preferential accumulation of P in grains [101].

Nevertheless, the relative dearth of information has led to few varieties of wheat being studied in regards to grain total P and PA. It is still unclear whether transportation of P to the grain occurs directly from phloem or via xylem through recycling from roots, and to what extent translocation of P between plant organs is altered at different P-regimes [102]. In wheat, only two significant transgenic studies that include over-expression of *TaPHR1-A1* and knockout of *TaPHO2-A1* were able to achieve enhanced P uptake and grain yield under low Pi condition [47,49]. It is reasonable to speculate that manipulating these Pi-related genes, among others yet to be discovered, will allow intentional modulation of Pi loading in grains [20,88].

Although the current knowledge of *PHT* expression and that of other regulators in seeds is in its early stage across plant species, some rice transporters demonstrate function in seed filling with Pi. A recent study investigating suppression of rice *OsPHT1;8* suggested its role in P redistribution and allocation of Pi in both embryo and endosperm seed tissue [94]. Hence, it will be important to implement such functional strategies for addressing transport and accumulation of Pi into grains [20].

5. Conclusions

It has been reported that plants use only 20%–30% of the Pi fertilizers applied to soil [103]. The significant remaining Pi is lost and can leach into aquatic ecosystems, instigating ecological issues such as eutrophication. Thus, it is clear that the excessive use of Pi fertilizers is not only an unsustainable and costly practice, but also ecologically unfriendly. Therefore, research on Pi nutrition

in plants should lead to changes in agricultural practices that would be both economically and environmentally beneficial.

How societally pertinent crop plants such as wheat maintain P homeostasis and respond to changes of Pi concentration remain poorly understood. Improving wheat Pi nutrition will require a full understanding of the physiology and molecular regulation of P remobilization from vegetative tissues to grains. In the future, it will be interesting to identify the complete list of genes that are involved in Pi transport between different wheat grain tissues, Pi acquisition, and Pi mobilization in embryo development. Although some uptake Pi transporters were discovered through classical molecular approaches, their regulatory mechanisms at the transcriptional and posttranscriptional levels remain obscure. This is particularly challenging in wheat because of the current unavailability of the complete genomic sequence. For the ones identified, the availability of sequenced mutant populations [104] alongside current genome editing tools like Clustered regularly interspaced short palindromic repeats-Cas9 technology will constitute an invaluable resource for their functional validation. In addition, a proper combination of omics approaches (such as RNA-seq), empowered with system biology tools, will help to construct regulatory pathways regulating Pi accumulation in wheat during its different developmental stages. Gaining this knowledge is vital to create crop varieties with improved P-use efficiency and modulate the Pi accumulation in grain.

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References

1. Dessibourg, O. Arsenic-based bacteria point to new life forms. *New Sci.* **2010**, *18*, 2.
2. Heuer, S.; Gaxiola, R.; Schilling, R.; Herrera-Estrella, L.; López-Arredondo, D.; Wissuwa, M.; Delhaize, E.; Rouached, H. Improving phosphorus use efficiency: A complex trait with emerging opportunities. *Plant J.* **2017**, *90*, 868–885. [CrossRef] [PubMed]
3. Lott, J.N.; Ockenden, I.; Raboy, V.; Batten, G.D. Phytic acid and phosphorus in crop seeds and fruits: A global estimate. *Seed Sci. Res.* **2000**, *10*, 11–33.
4. Runge-Metzger, A. Closing the cycle: Obstacles to efficient P management for improved global food security. *Scope-Sci. Comm. Probl. Environ. Int. Counc. Sci. Unions* **1995**, *54*, 27–42.
5. MacDonald, G.K.; Bennett, E.M.; Potter, P.A.; Ramankutty, N. Agronomic phosphorus imbalances across the world's croplands. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 3086–3091. [CrossRef] [PubMed]
6. Bouain, N.; Shahzad, Z.; Rouached, A.; Khan, G.A.; Berthomieu, P.; Abdelly, C.; Poirier, Y.; Rouached, H. Phosphate and zinc transport and signalling in plants: Toward a better understanding of their homeostasis interaction. *J. Exp. Bot.* **2014**, *65*, 5725–5741. [CrossRef] [PubMed]
7. Mongon, J.; Chaiwong, N.; Bouain, N.; Prom-u-Thai, C.; Secco, D.; Rouached, H. Phosphorus and Iron Deficiencies Influences Rice Shoot Growth in an Oxygen Dependent Manner: Insight from Upland and Lowland Rice. *Int. J. Mol. Sci.* **2017**, *18*, 607. [CrossRef] [PubMed]
8. Rouached, H.; Rhee, S.Y. System-level understanding of plant mineral nutrition in the big data era. *Curr. Opin. Syst. Biol.* **2017**, *4*, 71–77. [CrossRef]
9. Van Kauwenbergh, S.J. *World Phosphate Rock Reserves and Resources*; IFDC: Muscle Shoals, AL, USA, 2010.
10. Van Vuuren, D.P.; Bouwman, A.F.; Beusen, A.H. Phosphorus demand for the 1970–2100 period: A scenario analysis of resource depletion. *Glob. Environ. Chang.* **2010**, *20*, 428–439. [CrossRef]
11. Vance, C.P.; Uhde-Stone, C.; Allan, D.L. Phosphorus acquisition and use: Critical adaptations by plants for securing a nonrenewable resource. *New Phytol.* **2003**, *157*, 423–447. [CrossRef]

12. Lott, J.N.; Kolasa, J.; Batten, G.D.; Campbell, L.C. The critical role of phosphorus in world production of cereal grains and legume seeds. *Food Secur.* **2011**, *3*, 451–462. [CrossRef]

13. Walan, P.; Davidsson, S.; Johansson, S.; Höök, M. Phosphate rock production and depletion: Regional disaggregated modeling and global implications. *Resour. Conserv. Recycl.* **2014**, *93*, 178–187. [CrossRef]

14. Abelson, P.H. A potential phosphate crisis. *Science* **1999**, *283*, 2015. [CrossRef] [PubMed]

15. Cordell, D.; Drangert, J.-O.; White, S. The story of phosphorus: Global food security and food for thought. *Glob. Environ. Chang.* **2009**, *19*, 292–305. [CrossRef]

16. Ray, D.K.; Ramankutty, N.; Mueller, N.D.; West, P.C.; Foley, J.A. Recent patterns of crop yield growth and stagnation. *Nat. Commun.* **2012**, *3*, 1293. [CrossRef] [PubMed]

17. Rouached, H.; Arpat, A.B.; Poirier, Y. Regulation of phosphate starvation responses in plants: Signaling players and cross-talks. *Mol. Plant* **2010**, *3*, 288–299. [CrossRef] [PubMed]

18. Bouain, N.; Doumas, P.; Rouached, H. Recent advances in understanding the molecular mechanisms regulating the root system response to phosphate deficiency in Arabidopsis. *Curr. Genom.* **2016**, *17*, 308–314. [CrossRef] [PubMed]

19. Shin, H.; Shin, H.S.; Dewbre, G.R.; Harrison, M.J. Phosphate transport in Arabidopsis: Pht1; 1 and Pht1; 4 play a major role in phosphate acquisition from both low-and high-phosphate environments. *Plant J.* **2004**, *39*, 629–642. [CrossRef] [PubMed]

20. Shukla, V.; Kaur, M.; Aggarwal, S.; Bhati, K.K.; Kaur, J.; Mantri, S.; Pandey, A.K. Tissue specific transcript profiling of wheat phosphate transporter genes and its association with phosphate allocation in grains. *Sci. Rep.* **2016**, *6*. [CrossRef] [PubMed]

21. Teng, W.; Zhao, Y.-Y.; Zhao, X.-Q.; He, X.; Ma, W.-Y.; Deng, Y.; Chen, X.-P.; Tong, Y.-P. Genome-wide Identification, Characterization, and Expression Analysis of PHT1 Phosphate Transporters in Wheat. *Front. Plant Sci.* **2017**, *8*. [CrossRef] [PubMed]

22. Grün, A.; Buchner, P.; Broadley, M.R.; Hawkesford, M.J. Identification and expression profiling of Pht1 phosphate transporters in wheat in controlled environments and in the field. *Plant Biol.* **2017**. [CrossRef] [PubMed]

23. Veneklaas, E.J.; Lambers, H.; Bragg, J.; Finnegan, PM.; Lovelock, CE.; Plaxton, W.C.; Price, C.A.; Scheible, W.R.; Shane, M.W.; White, P.J.; et al. Opportunities for improving phosphorus-use efficiency in crop plants. *New Phytol.* **2012**, *195*, 306–320. [CrossRef] [PubMed]

24. Koornneef, M.; Meinke, D. The development of Arabidopsis as a model plant. *Plant J.* **2010**, *61*, 909–921. [CrossRef] [PubMed]

25. Nussaume, L.; Kanno, S.; Javot, H.; Marin, E.; Pochon, N.; Ayadi, A.; Nakanishi, T.M.; Thibaud, M.-C. Phosphate import in plants: Focus on the PHT1 transporters. *Front. Plant Sci.* **2011**, *2*, 83. [CrossRef] [PubMed]

26. Liu, J.; Yang, L.; Luan, M.; Wang, Y.; Zhang, C.; Zhang, B.; Shi, J.; Zhao, F.-G.; Lan, W.; Luan, S. A vacuolar phosphate transporter essential for phosphate homeostasis in Arabidopsis. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, E6571–E6578. [CrossRef] [PubMed]

27. Hamburger, D.; Rezzonico, E.; Petétot, J.M.-C.; Somerville, C.; Poirier, Y. Identification and characterization of the Arabidopsis *PHO1* gene involved in phosphate loading to the xylem. *Plant Cell* **2002**, *14*, 889–902. [CrossRef] [PubMed]

28. Stefanovic, A.; Ribot, C.; Rouached, H.; Wang, Y.; Chong, J.; Belbahri, L.; Delessert, S.; Poirier, Y. Members of the *PHO1* gene family show limited functional redundancy in phosphate transfer to the shoot, and are regulated by phosphate deficiency via distinct pathways. *Plant J.* **2007**, *50*, 982–994. [CrossRef] [PubMed]

29. Secco, D.; Bouain, N.; Rouached, A.; Prom-U-Thai, C.; Hanin, M.; Pandey, A.K.; Rouached, H. Phosphate, phytate and phytases in plants: From fundamental knowledge gained in Arabidopsis to potential biotechnological applications in wheat. *Crit. Rev. Biotechnol.* **2017**, *37*, 898–910. [CrossRef] [PubMed]

30. Hassler, S.; Lemke, L.; Jung, B.; Möhlmann, T.; Krüger, F.; Schumacher, K.; Espen, L.; Martinoia, E.; Neuhaus, H.E. Lack of the Golgi phosphate transporter PHT4; 6 causes strong developmental defects, constitutively activated disease resistance mechanisms and altered intracellular phosphate compartmentation in Arabidopsis. *Plant J.* **2012**, *72*, 732–744. [CrossRef] [PubMed]

31. Jia, F.; Wan, X.; Zhu, W.; Sun, D.; Zheng, C.; Liu, P.; Huang, J. Overexpression of mitochondrial phosphate transporter 3 severely hampers plant development through regulating mitochondrial function in Arabidopsis. *PLoS ONE* **2015**, *10*, e0129717. [CrossRef] [PubMed]

32. Miura, K.; Rus, A.; Sharkhuu, A.; Yokoi, S.; Karthikeyan, A.S.; Raghothama, K.G.; Baek, D.; Koo, Y.D.; Jin, J.B.; Bressan, R.A. The Arabidopsis SUMO E3 ligase SIZ1 controls phosphate deficiency responses. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 7760–7765. [CrossRef] [PubMed]

33. Duan, K.; Yi, K.; Dang, L.; Huang, H.; Wu, W.; Wu, P. Characterization of a sub-family of Arabidopsis genes with the SPX domain reveals their diverse functions in plant tolerance to phosphorus starvation. *Plant J.* **2008**, *54*, 965–975. [CrossRef] [PubMed]

34. Puga, M.I.; Mateos, I.; Charukesi, R.; Wang, Z.; Franco-Zorrilla, J.M.; de Lorenzo, L.; Irigoyen, M.L.; Masiero, S.; Bustos, R.; Rodríguez, J. SPX1 is a phosphate-dependent inhibitor of PHOSPHATE STARVATION RESPONSE 1 in Arabidopsis. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 14947–14952. [CrossRef] [PubMed]

35. Oono, Y.; Kobayashi, F.; Kawahara, Y.; Yazawa, T.; Handa, H.; Itoh, T.; Matsumoto, T. Characterisation of the wheat (*Triticum aestivum* L.) transcriptome by de novo assembly for the discovery of phosphate starvation-responsive genes: Gene expression in Pi-stressed wheat. *BMC Genom.* **2013**, *14*, 77. [CrossRef] [PubMed]

36. Kuo, H.F.; Chang, T.Y.; Chiang, S.F.; Wang, W.D.; Charng, Y.Y.; Chiou, T.J. Arabidopsis inositol pentakisphosphate 2-kinase, AtIPK1, is required for growth and modulates phosphate homeostasis at the transcriptional level. *Plant J.* **2014**, *80*, 503–515. [CrossRef] [PubMed]

37. Bhati, K.K.; Aggarwal, S.; Sharma, S.; Mantri, S.; Singh, S.P.; Bhalla, S.; Kaur, J.; Tiwari, S.; Roy, J.K.; Tuli, R. Differential expression of structural genes for the late phase of phytic acid biosynthesis in developing seeds of wheat (*Triticum aestivum* L.). *Plant Sci.* **2014**, *224*, 74–85. [CrossRef] [PubMed]

38. Rausch, C.; Bucher, M. Molecular mechanisms of phosphate transport in plants. *Planta* **2002**, *216*, 23–37. [CrossRef] [PubMed]

39. Davies, T.; Ying, J.; Xu, Q.; Li, Z.; Li, J.; Gordon-Weeks, R. Expression analysis of putative high-affinity phosphate transporters in Chinese winter wheats. *Plant Cell Environ.* **2002**, *25*, 1325–1339. [CrossRef]

40. Daram, P.; Brunner, S.; Rausch, C.; Steiner, C.; Amrhein, N.; Bucher, M. Pht2; 1 encodes a low-affinity phosphate transporter from Arabidopsis. *Plant Cell* **1999**, *11*, 2153–2166. [CrossRef] [PubMed]

41. Guo, C.; Zhao, X.; Liu, X.; Zhang, L.; Gu, J.; Li, X.; Lu, W.; Xiao, K. Function of wheat phosphate transporter gene TaPHT2; 1 in Pi translocation and plant growth regulation under replete and limited Pi supply conditions. *Planta* **2013**, *237*, 1163–1178. [CrossRef] [PubMed]

42. Poirier, Y.; Bucher, M. Phosphate transport and homeostasis in Arabidopsis. *Arabidopsis Book* **2002**, e0024. [CrossRef] [PubMed]

43. Zhu, W.; Miao, Q.; Sun, D.; Yang, G.; Wu, C.; Huang, J.; Zheng, C. The mitochondrial phosphate transporters modulate plant responses to salt stress via affecting ATP and gibberellin metabolism in Arabidopsis thaliana. *PLoS ONE* **2012**, *7*, e43530. [CrossRef] [PubMed]

44. Aziz, T.; Finnegan, P.M.; Lambers, H.; Jost, R. Organ-specific phosphorus-allocation patterns and transcript profiles linked to phosphorus efficiency in two contrasting wheat genotypes. *Plant Cell Environ.* **2014**, *37*, 943–960. [CrossRef] [PubMed]

45. Guo, B.; Jin, Y.; Wussler, C.; Blancaflor, E.; Motes, C.; Versaw, W.K. Functional analysis of the Arabidopsis PHT4 family of intracellular phosphate transporters. *New Phytol.* **2008**, *177*, 889–898. [CrossRef] [PubMed]

46. Liu, T.-Y.; Huang, T.-K.; Yang, S.-Y.; Hong, Y.-T.; Huang, S.-M.; Wang, F.-N.; Chiang, S.-F.; Tsai, S.-Y.; Lu, W.-C.; Chiou, T.-J. Identification of plant vacuolar transporters mediating phosphate storage. *Nat. Commun.* **2016**, *7*, 111.95. [CrossRef] [PubMed]

47. Ouyang, X.; Hong, X.; Zhao, X.; Zhang, W.; He, X.; Ma, W.; Teng, W.; Tong, Y. Knock out of the PHOSPHATE 2 gene TaPHO2-A1 improves phosphorus uptake and grain yield under low phosphorus conditions in common wheat. *Sci. Rep.* **2016**, *6*, 29850. [CrossRef] [PubMed]

48. Rubio, V.; Linhares, F.; Solano, R.; Martín, A.C.; Iglesias, J.; Leyva, A.; Paz-Ares, J. A conserved MYB transcription factor involved in phosphate starvation signaling both in vascular plants and in unicellular algae. *Genes Dev.* **2001**, *15*, 2122–2133. [CrossRef] [PubMed]

49. Wang, J.; Sun, J.; Miao, J.; Guo, J.; Shi, Z.; He, M.; Chen, Y.; Zhao, X.; Li, B.; Han, F. A phosphate starvation response regulator Ta-PHR1 is involved in phosphate signalling and increases grain yield in wheat. *Ann. Bot.* **2013**, *111*, 1139–1153. [CrossRef] [PubMed]

50. Bustos, R.; Castrillo, G.; Linhares, F.; Puga, M.I.; Rubio, V.; Pérez-Pérez, J.; Solano, R.; Leyva, A.; Paz-Ares, J. A central regulatory system largely controls transcriptional activation and repression responses to phosphate starvation in Arabidopsis. *PLoS Genet.* **2010**, *6*, e1001102. [CrossRef] [PubMed]

51. González, E.; Solano, R.; Rubio, V.; Leyva, A.; Paz-Ares, J. PHOSPHATE TRANSPORTER TRAFFIC FACILITATOR1 is a plant-specific SEC12-related protein that enables the endoplasmic reticulum exit of a high-affinity phosphate transporter in Arabidopsis. *Plant Cell* **2005**, *17*, 3500–3512. [CrossRef] [PubMed]

52. Rouached, H.; Stefanovic, A.; Secco, D.; Arpat, A.B.; Gout, E.; Bligny, R.; Poirier, Y. Uncoupling phosphate deficiency from its major effects on growth and transcriptome via PHO1 expression in Arabidopsis. *Plant J.* **2011**, *65*, 557–570. [CrossRef] [PubMed]

53. Bari, R.; Pant, B.D.; Stitt, M.; Scheible, W.-R. PHO2, microRNA399, and PHR1 define a phosphate-signaling pathway in plants. *Plant Physiol.* **2006**, *141*, 988–999. [CrossRef] [PubMed]

54. Devaiah, B.N.; Nagarajan, V.K.; Raghothama, K.G. Phosphate homeostasis and root development in Arabidopsis are synchronized by the zinc finger transcription factor ZAT6. *Plant Physiol.* **2007**, *145*, 147–159. [CrossRef] [PubMed]

55. Smith, A.P.; Jain, A.; Deal, R.B.; Nagarajan, V.K.; Poling, M.D.; Raghothama, K.G.; Meagher, R.B. Histone H2A. Z regulates the expression of several classes of phosphate starvation response genes but not as a transcriptional activator. *Plant Physiol.* **2010**, *152*, 217–225. [CrossRef] [PubMed]

56. Chen, Y.-F.; Li, L.-Q.; Xu, Q.; Kong, Y.-H.; Wang, H.; Wu, W.-H. The WRKY6 transcription factor modulates PHOSPHATE1 expression in response to low Pi stress in Arabidopsis. *Plant Cell* **2009**, *21*, 3554–3566. [CrossRef] [PubMed]

57. Su, T.; Xu, Q.; Zhang, F.-C.; Chen, Y.; Li, L.-Q.; Wu, W.-H.; Chen, Y.-F. WRKY42 modulates phosphate homeostasis through regulating phosphate translocation and acquisition in Arabidopsis. *Plant Physiol.* **2015**, *167*, 1579–1591. [CrossRef] [PubMed]

58. Wang, H.; Xu, Q.; Kong, Y.-H.; Chen, Y.; Duan, J.-Y.; Wu, W.-H.; Chen, Y.-F. Arabidopsis WRKY45 transcription factor activates PHOSPHATE TRANSPORTER1; 1 expression in response to phosphate starvation. *Plant Physiol.* **2014**, *164*, 2020–2029. [CrossRef] [PubMed]

59. Devaiah, B.N.; Karthikeyan, A.S.; Raghothama, K.G. WRKY75 transcription factor is a modulator of phosphate acquisition and root development in Arabidopsis. *Plant Physiol.* **2007**, *143*, 1789–1801. [CrossRef] [PubMed]

60. Lin, W.-Y.; Huang, T.-K.; Chiou, T.-J. Nitrogen Limitation Adaptation, a target of microRNA827, mediates degradation of plasma membrane–localized phosphate transporters to maintain phosphate homeostasis in Arabidopsis. *Plant Cell* **2013**, *25*, 4061–4074. [CrossRef] [PubMed]

61. Wu, P.; Ma, L.; Hou, X.; Wang, M.; Wu, Y.; Liu, F.; Deng, X.W. Phosphate starvation triggers distinct alterations of genome expression in Arabidopsis roots and leaves. *Plant Physiol.* **2003**, *132*, 1260–1271. [CrossRef] [PubMed]

62. Huang, T.-K.; Han, C.-L.; Lin, S.-I.; Chen, Y.-J.; Tsai, Y.-C.; Chen, Y.-R.; Chen, J.-W.; Lin, W.-Y.; Chen, P.-M.; Liu, T.-Y. Identification of downstream components of ubiquitin-conjugating enzyme PHOSPHATE2 by quantitative membrane proteomics in Arabidopsis roots. *Plant Cell* **2013**, *25*, 4044–4060. [CrossRef] [PubMed]

63. Kant, S.; Peng, M.; Rothstein, S.J. Genetic regulation by NLA and microRNA827 for maintaining nitrate-dependent phosphate homeostasis in Arabidopsis. *PLoS Genet.* **2011**, *7*, e1002021. [CrossRef] [PubMed]

64. Cardona-López, X.; Cuyas, L.; Marín, E.; Rajulu, C.; Irigoyen, M.L.; Gil, E.; Puga, M.I.; Bligny, R.; Nussaume, L.; Geldner, N. ESCRT-III-associated protein ALIX mediates high-affinity phosphate transporter trafficking to maintain phosphate homeostasis in Arabidopsis. *Plant Cell* **2015**, *27*, 2560–2581. [CrossRef] [PubMed]

65. Guo, C.; Guo, L.; Li, X.; Gu, J.; Zhao, M.; Duan, W.; Ma, C.; Lu, W.; Xiao, K. TaPT2, a high-affinity phosphate transporter gene in wheat (*Triticum aestivum* L.), is crucial in plant Pi uptake under phosphorus deprivation. *Acta Physiol. Plant.* **2014**, *36*, 1373–1384. [CrossRef]

66. Bayle, V.; Arrighi, J.-F.; Creff, A.; Nespoulous, C.; Vialaret, J.; Rossignol, M.; Gonzalez, E.; Paz-Ares, J.; Nussaume, L. Arabidopsis thaliana high-affinity phosphate transporters exhibit multiple levels of posttranslational regulation. *Plant Cell Online* **2011**, *23*, 1523–1535. [CrossRef] [PubMed]

67. Wege, S.; Khan, G.A.; Jung, J.-Y.; Vogiatzaki, E.; Pradervand, S.; Aller, I.; Meyer, A.J.; Poirier, Y. The EXS domain of PHO1 participates in the response of shoots to phosphate deficiency via a root-to-shoot signal. *Plant Physiol.* **2016**, *170*, 385–400. [CrossRef] [PubMed]

68. Krouk, G.; Lacombe, B.; Bielach, A.; Perrine-Walker, F.; Malinska, K.; Mounier, E.; Hoyerova, K.; Tillard, P.; Leon, S.; Ljung, K. Nitrate-regulated auxin transport by NRT1. 1 defines a mechanism for nutrient sensing in plants. *Dev. Cell* **2010**, *18*, 927–937. [CrossRef] [PubMed]

69. Lin, W.-Y.; Lin, S.-I.; Chiou, T.-J. Molecular regulators of phosphate homeostasis in plants. *J. Exp. Bot.* **2009**, *60*, 1427–1438. [CrossRef] [PubMed]

70. Misson, J.; Thibaud, M.-C.; Bechtold, N.; Raghothama, K.; Nussaume, L. Transcriptional regulation and functional properties of Arabidopsis Pht1; 4, a high affinity transporter contributing greatly to phosphate uptake in phosphate deprived plants. *Plant Mol. Biol.* **2004**, *55*, 727–741. [CrossRef] [PubMed]

71. Wild, R.; Gerasimaite, R.; Jung, J.-Y.; Truffault, V.; Pavlovic, I.; Schmidt, A.; Saiardi, A.; Jessen, H.J.; Poirier, Y.; Hothorn, M. Control of eukaryotic phosphate homeostasis by inositol polyphosphate sensor domains. *Science* **2016**, *352*, 986–990. [CrossRef] [PubMed]

72. Liu, T.-Y.; Huang, T.-K.; Tseng, C.-Y.; Lai, Y.-S.; Lin, S.-I.; Lin, W.-Y.; Chen, J.-W.; Chiou, T.-J. PHO2-dependent degradation of PHO1 modulates phosphate homeostasis in Arabidopsis. *Plant Cell* **2012**, *24*, 2168–2218. [CrossRef] [PubMed]

73. Briat, J.-F.; Rouached, H.; Tissot, N.; Gaymard, F.; Dubos, C. Integration of P, S, Fe, and Zn nutrition signals in Arabidopsis thaliana: Potential involvement of PHOSPHATE STARVATION RESPONSE 1 (PHR1). *Front. Plant Sci.* **2015**, *6*, 290. [CrossRef] [PubMed]

74. Aung, K.; Lin, S.-I.; Wu, C.-C.; Huang, Y.-T.; Su, C.-l.; Chiou, T.-J. PHO2, a phosphate overaccumulator, is caused by a nonsense mutation in a microRNA399 target gene. *Plant Physiol.* **2006**, *141*, 1000–1011. [CrossRef] [PubMed]

75. Hu, B.; Zhu, C.; Li, F.; Tang, J.; Wang, Y.; Lin, A.; Liu, L.; Che, R.; Chu, C. LEAF TIP NECROSIS1 plays a pivotal role in the regulation of multiple phosphate starvation responses in rice. *Plant Physiol.* **2011**, *156*, 1101–1115. [CrossRef] [PubMed]

76. Khan, G.A.; Bouraine, S.; Wege, S.; Li, Y.; de Carbonnel, M.; Berthomieu, P.; Poirier, Y.; Rouached, H. Coordination between zinc and phosphate homeostasis involves the transcription factor PHR1, the phosphate exporter PHO1, and its homologue PHO1; H3 in Arabidopsis. *J. Exp. Bot.* **2014**, *65*, 871–884. [CrossRef] [PubMed]

77. Kisko, M.; Bouain, N.; Rouached, A.; Choudhary, S.P.; Rouached, H. Molecular mechanisms of phosphate and zinc signalling crosstalk in plants: Phosphate and zinc loading into root xylem in Arabidopsis. *Environ. Exp. Bot.* **2015**, *114*, 57–64. [CrossRef]

78. Ova, E.A.; Kutman, U.B.; Ozturk, L.; Cakmak, I. High phosphorus supply reduced zinc concentration of wheat in native soil but not in autoclaved soil or nutrient solution. *Plant Soil* **2015**, *393*, 147–162. [CrossRef]

79. Pal, S.; Kisko, M.; Dubos, C.; Lacombe, B.; Berthomieu, P.; Krouk, G.; Rouached, H. TransDetect identifies a new regulatory module controlling phosphate accumulation. *Plant Physiol.* **2017**, *175*, 916–926. [CrossRef] [PubMed]

80. Rouached, H. Recent developments in plant zinc homeostasis and the path toward improved biofortification and phytoremediation programs. *Plant Signal. Behav.* **2013**, *8*, e22681. [CrossRef] [PubMed]

81. White, P.J. Veneklaas Erik, J. Nature and nurture: The importance of seed phosphorus content. *Plant Soil* **2012**, *357*, 1–8. [CrossRef]

82. Fan, Y.; Van den Dool, H. A global monthly land surface air temperature analysis for 1948–present. *J. Geophys. Res. Atmos.* **2008**, *113*. [CrossRef]

83. DeFries, R.; Fanzo, J.; Remans, R.; Palm, C.; Wood, S.; Anderman, T.L. Metrics for land-scarce agriculture. *Science* **2015**, *349*, 238–240. [CrossRef] [PubMed]

84. Dietterich, L.H.; Zanobetti, A.; Kloog, I.; Huybers, P.; Leakey, A.D.; Bloom, A.J.; Carlisle, E.; Fernando, N.; Fitzgerald, G.; Hasegawa, T. Impacts of elevated atmospheric CO_2 on nutrient content of important food crops. *Sci. Data* **2015**, *2*, 150063. [CrossRef] [PubMed]

85. Belgaroui, N.; Zaidi, I.; Farhat, A.; Chouayekh, H.; Bouain, N.; Chay, S.; Curie, C.; Mari, S.; Masmoudi, K.; Davidian, J.-C. Over-expression of the bacterial phytase US417 in Arabidopsis reduces the concentration of phytic acid and reveals its involvement in the regulation of sulfate and phosphate homeostasis and signaling. *Plant Cell Physiol.* **2014**, *55*, 1912–1924. [CrossRef] [PubMed]

86. Wang, F.; Rose, T.; Jeong, K.; Kretzschmar, T.; Wissuwa, M. The knowns and unknowns of phosphorus loading into grains, and implications for phosphorus efficiency in cropping systems. *J. Exp. Bot.* **2015**, *67*, 1221–1229. [CrossRef] [PubMed]

87. Zhang, F.; Sun, Y.; Pei, W.; Jain, A.; Sun, R.; Cao, Y.; Wu, X.; Jiang, T.; Zhang, L.; Fan, X. Involvement of OsPht1; 4 in phosphate acquisition and mobilization facilitates embryo development in rice. *Plant J.* **2015**, *82*, 556–569. [CrossRef] [PubMed]

88. Vogiatzaki, E.; Baroux, C.; Jung, J.-Y.; Poirier, Y. PHO1 exports phosphate from the chalazal seed coat to the embryo in developing Arabidopsis seeds. *Curr. Biol.* **2017**, *27*, 2893–2900. [CrossRef] [PubMed]

89. Batten, G.; Wardlaw, I. Senescence and grain development in wheat plants grown with contrasting phosphorus regimes. *Aust. J. Plant Physiol.* **1987**, *14*, 253–265. [CrossRef]

90. Raboy, V. Approaches and challenges to engineering seed phytate and total phosphorus. *Plant Sci.* **2009**, *177*, 281–296. [CrossRef]

91. Sparvoli, F.; Cominelli, E. Seed biofortification and phytic acid reduction: A conflict of interest for the plant? *Plants* **2015**, *4*, 728–755. [CrossRef] [PubMed]

92. Zhang, Y.-Q.; Sun, Y.-X.; Ye, Y.-L.; Karim, M.R.; Xue, Y.-F.; Yan, P.; Meng, Q.-F.; Cui, Z.-L.; Cakmak, I.; Zhang, F.-S. Zinc biofortification of wheat through fertilizer applications in different locations of China. *Field Crops Res.* **2012**, *125*, 1–7. [CrossRef]

93. Raboy, V.; Cichy, K.; Peterson, K.; Reichman, S.; Sompong, U.; Srinives, P.; Saneoka, H. Barley (*Hordeum vulgare* L.) low phytic acid 1–1: An endosperm-specific, filial determinant of seed total phosphorus. *J. Hered.* **2014**, *105*, 656–665. [CrossRef] [PubMed]

94. Li, Y.; Zhang, J.; Zhang, X.; Fan, H.; Gu, M.; Qu, H.; Xu, G. Phosphate transporter OsPht1; 8 in rice plays an important role in phosphorus redistribution from source to sink organs and allocation between embryo and endosperm of seeds. *Plant Sci.* **2015**, *230*, 23–32. [CrossRef] [PubMed]

95. Shi, J.; Wang, H.; Schellin, K.; Li, B.; Faller, M.; Stoop, J.M.; Meeley, R.B.; Ertl, D.S.; Ranch, J.P.; Glassman, K. Embryo-specific silencing of a transporter reduces phytic acid content of maize and soybean seeds. *Nat. Biotechnol.* **2007**, *25*, 930–937. [CrossRef] [PubMed]

96. Bhati, K.K.; Alok, A.; Kumar, A.; Kaur, J.; Tiwari, S.; Pandey, A.K. Silencing of ABCC13 transporter in wheat reveals its involvement in grain development, phytic acid accumulation and lateral root formation. *J. Exp. Bot.* **2016**, *67*, 4379–4389. [CrossRef] [PubMed]

97. Ali, N.; Paul, S.; Gayen, D.; Sarkar, S.N.; Datta, K.; Datta, S.K. Development of low phytate rice by RNAi mediated seed-specific silencing of inositol 1, 3, 4, 5, 6-pentakisphosphate 2-kinase gene (IPK1). *PLoS ONE* **2013**, *8*, e68161. [CrossRef] [PubMed]

98. Ali, N.; Paul, S.; Gayen, D.; Sarkar, S.N.; Datta, S.K.; Datta, K. RNAi mediated down regulation of myo-inositol-3-phosphate synthase to generate low phytate rice. *Rice* **2013**, *6*, 12. [CrossRef] [PubMed]

99. Li, Z.; Zhang, X.; Zhao, Y.; Li, Y.; Zhang, G.; Peng, Z.; Zhang, J. Enhancing auxin accumulation in maize root tips improves root growth and dwarfs plant height. *Plant Biotechnol. J.* **2018**, *16*, 86–99. [CrossRef] [PubMed]

100. Zhao, H.; Frank, T.; Tan, Y.; Zhou, C.; Jabnoune, M.; Arpat, A.B.; Cui, H.; Huang, J.; He, Z.; Poirier, Y. Disruption of OsSULTR3; 3 reduces phytate and phosphorus concentrations and alters the metabolite profile in rice grains. *New Phytol.* **2016**, *211*, 926–939. [CrossRef] [PubMed]

101. Yamaji, N.; Takemoto, Y.; Miyaji, T.; Mitani-Ueno, N.; Yoshida, K.T.; Ma, J.F. Reducing phosphorus accumulation in rice grains with an impaired transporter in the node. *Nature* **2017**, *541*, 92–95. [CrossRef] [PubMed]

102. Peng, Z.; Li, C. Transport and partitioning of phosphorus in wheat as affected by P withdrawal during flag-leaf expansion. *Plant Soil* **2005**, *268*, 1–11. [CrossRef]

103. Syers, K.; Johnston, A.E.; Curtin, D. *Efficiency of Soil and Fertilizer Phosphorus Use: Reconciling Changing Concepts of Soils Phosphorus Behaviour with Agronomic Information*; FAO Fertilizer and Plant Nutrition Bulletin 18; Food and Agriculture Organization of the United Nations: Rome, Italy, 2008.

104. Krasileva, K.V.; Vasquez-Gross, H.A.; Howell, T.; Bailey, P.; Paraiso, F.; Clissold, L.; Simmonds, J.; Ramirez-Gonzalez, R.H.; Wang, X.; Borrill, P. Uncovering hidden variation in polyploid wheat. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, E913–E921. [CrossRef] [PubMed]