agriculture

MDPI

Review

Advances in the Biological Functions of Auxin Transporters in Rice

Yaning Feng [1,2], Enhe Bayaer [1,*] and Yanhua Qi [1,2,*]

[1] College of Life Science and Technology, Inner Mongolia Normal University, Hohhot 010022, China; 20204018025@mails.imnu.edu.cn
[2] Key Laboratory of Herbage & Endemic Crop Biology of Ministry of Education, Inner Mongolia Key Laboratory of Herbage & Endemic Crop Biotechnology, School of Life Sciences, Inner Mongolia University, Hohhot 010030, China
* Correspondence: nmsdenhe@imnu.edu.cn (E.B.); qyhjp@zju.edu.cn (Y.Q.)

Abstract: Auxin is the earliest discovered plant hormone, which plays important roles in each aspect of plant growth and development. There are two main pathways for auxin to be transported from the synthetic site (such as young leaves and terminal buds) to the active site. First, auxin is transported over long distances through phloem in an unfixed direction throughout the whole plant. Second, short-distance polar transport between cells requires the participation of auxin carriers, including unidirectional transport from stem tip to root and local unidirectional transport between tissues. Polar transport is critical to the establishment and maintenance of the auxin concentration gradient, which specifically regulates plant growth and development and responds to environmental changes. In this article, we reviewed the research progress of auxin transporters AUX1/LAX, PIN, and ABCB families, and some potential auxin transporters in rice growth and development, which provide information for the interpretation of biological functions of polar auxin transport families and lay a foundation for the genetic improvement of important agronomic traits in rice.

Keywords: auxin; AUX1/LAX; PIN; ABCB; polar auxin transport; rice

Citation: Feng, Y.; Bayaer, E.; Qi, Y. Advances in the Biological Functions of Auxin Transporters in Rice. *Agriculture* **2022**, *12*, 989. https://doi.org/10.3390/agriculture12070989

Academic Editor: Mingcai Zhang

Received: 28 April 2022
Accepted: 6 July 2022
Published: 9 July 2022

1. Introduction

Auxin is a very important plant hormone, acting on all aspects of plant growth and development, participating in the regulation of root formation, inflorescence and leaf sequence development, vascular tissue differentiation, apical dominance, fruit ripening, phototropism, and gravitropism [1–3]. Different auxin concentrations affect plant growth and development, and the maintenance of the auxin concentration gradient depends on polar transport. To date, three gene families involved in polar auxin transport have been reported: AUX1/LAX (auxin resistant 1/like aux1), PIN (PIN-formed), and ABCB/MDR/PGP (ATP binding cassette B/Multidrug-resistance/p-glycoprotein) [4–14]. The AUX1/LAX family is involved in auxin influx, the PIN family is involved in auxin efflux, and the ABCB family may be a bidirectional auxin transporter protein. There are currently many studies on the functions of auxin transporters in *Arabidopsis thaliana*. It has been reported that polar auxin transport plays an important role in the growth and development, participating in response to heavy metal stress of *Arabidopsis thaliana* [6,15,16]. For example, *AtLAX3* mediates auxin transport during the development of lateral root primordia [17]; *AtPIN4* is involved in the transport of auxin to the apical resting center [18]; *AtABCB4* has been proved to be a bidirectional auxin transporter, which is responsible for auxin influx when the intracellular auxin concentration is low and auxin efflux when it is high [19]. The biological functions of the *AUX1/LAX* gene and *PIN* gene in rice have been gradually reported, but there are very few reports on the biological function of the ABCB gene. Here, we summarize the characteristics of auxin transporters and the biofunctions of the *OsAUX*,

OsPIN, and *OsABCB* gene families acting upon root development, yield traits, and heavy metal stress in rice.

2. Auxin Transport Characteristics

Auxin is mainly synthesized in stem apical meristem, leaf primordium, flower primordium, and developing seeds where plants grow rapidly. Synthetic auxin needs to be transported to specific sites in order to function [20]. There are three modes of auxin transport in plants: non-polar transport, polar transport, and lateral transport (Figure 1). The non-polar transport relies on free diffusion and is transported in the phloem, like other compounds, at a transport speed of 1–2.4 cm/h, and the transport direction depends on the concentration difference between the two ends [21]. Polar transport is a unique mode of auxin transport, requiring carriers and energy consumption. It is a single-direction short-distance transport between cells with a transport speed of 5–20 mm/h, which can maintain the inverse concentration of auxin transport [22]. According to the different directions of polar auxin transport, it can be divided into acropetal translocation and basipetal translocation. Basipetal translocation refers to the auxin transport from the apex to the bottom, while the reverse is true for acropetal translocation. In the stems of higher plants, there is only basipetal translocation—that is, from the auxin synthesis point at the stem tip to the stem base. However, both pathways exist in the roots of higher plants; growth hormone is transported from the root to the root tip in the acropetal translocation mode, it is then reunited and redistributed with the synthetic auxin in the root tip, and then transported up from the cortex and epidermis of the root, which is the basipetal translocation in the root [21,23–25]. Lateral transport can only occur when unidirectional stimulation occurs in root tip, stem tip, and other parts of the plant, and transport is affected by gravity, light, and internal charge distribution [26]. When one side light is irradiated, the tip of plant organs is negatively charged to the light side, the backlight side is positively charged, and the free auxin anion moves to the backlight side with positive charge, thus completing the lateral transport of auxin. The backlight side has a high concentration of auxin, which promotes cell growth. Therefore, the backlight side grows faster, causing the tip of the plant to bend towards the light source [27]. According to the Cholodny—Went theory, when plants are laid horizontally, auxin will be transported laterally from the far end to the near end, and the concentration of auxin near the ground side of roots and stems is higher, resulting in the growth of roots in the direction of gravity and stem in the direction deviate from gravity [28]. For example, *OsLAZY1* regulates shoot gravitropism by affecting polar and lateral transport of auxin, which affects tiller angle [29]. *AtPIN3* can regulate the lateral transport of auxin in gravitropism reaction, so that auxin concentration gradients are formed at the near and far sides, resulting in gravitropism bending of hypocotyl in *Arabidopsis thaliana* [30]. When IAA or NAA was used to treat the near ground side of stolon, the gravity response was increased, and when IAA or NAA was used to treat the far ground side, the gravity response was inhibited. The gravity response of stolons treated with NPA (Naphthylphthalamic acid) or TIBA (2,3,5-Triidobenzoid acid) was weakened at the near and far sides, indicating that the gravity response of stolons was also affected after interfering with the lateral transport of IAA. It is speculated that the IAA content and lateral transport are closely related to the gravity response of stolons in *Chrysanthemum yantaiense* [31].

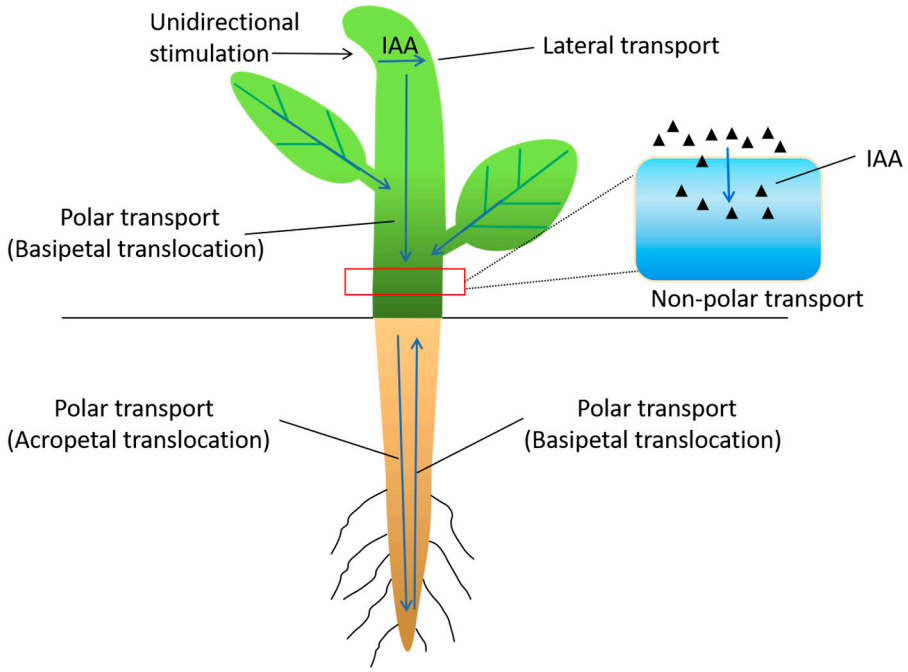

Figure 1. Three modes of auxin transport in plants: non-polar transport, polar transport, and lateral transport. The blue arrows indicate the direction of the auxin flow (refer to Jiang et al., 2011 [21]; Friml et al., 2002 [22]; Rashotte et al., 2000 [24]; Xu et al., 2012 [25]; Zou et al., 2018 [26]).

As for the mechanism of polar auxin transport, the chemical osmotic coupling model is generally accepted at present (Figure 2), which is formed on the basis of Raven's proposal that auxin transport between plant cells is closely related to PH value and the potential difference between the inside and outside of cells [32]. Proton pumps on the cell membrane release energy to pump H^+ into the cell wall by hydrolyzing ATP with ATPase, making the cell wall acidic (pH = 5.5). IAA molecules in the cell wall tends to be protonated (IAAH), which is in the form of a weak acid (pH 4.75) that is lipophilic, and can thus enter the cells through passive transport or co-operative diffusion. In the cytoplasm, auxin is neutral (pH 7.5) and dissociates to the auxin anion (IAA^-). Auxin has low lipophilicity and permeability. It is difficultly passed through the plasma membrane and can only be transported to the extracellular by the efflux carrier distributed on the plasma membrane. The asymmetric distribution of carriers on plasma membrane determines polar auxin transport. Studies have shown that the polar localization of the PIN protein on the plasma membrane is related to the direction of auxin transport and is an important reason for the asymmetric distribution of auxin in plants [13,33]. For example, in the process of root-oriented gravity reaction, the AtPIN2 protein was asymmetrically distributed on the upper and lower sides of the root tip, which induced the asymmetric distribution of auxin [34,35]. The polar transport is the unique transport model on auxin in plant hormones, mainly relying on three transport proteins: AUX1/LAX influx carrier, PIN efflux carrier, and ABCB/MDR/PGP influx/efflux carrier families [36,37].

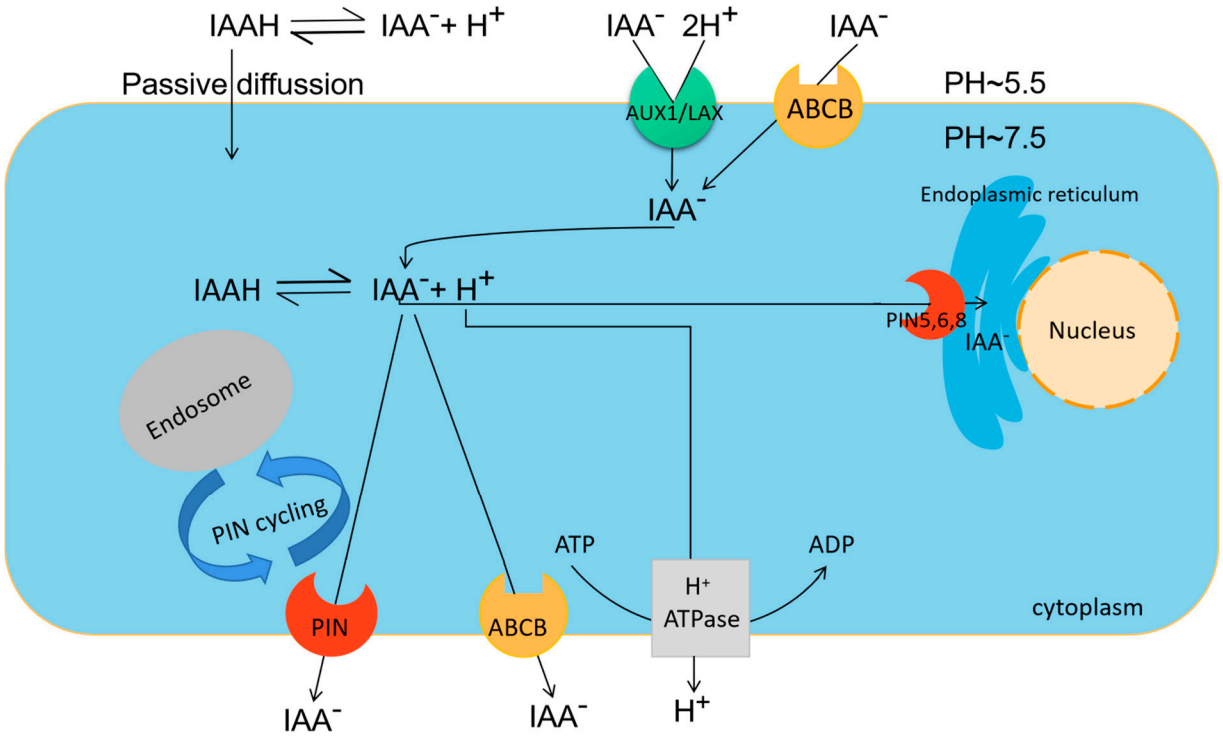

Figure 2. Chemiosmotic model for polar auxin transport. Auxin transporters include PIN, AUX1/LAX, and ABCB. Protonated IAA (IAAH) enters cells through passive transport, while auxin anion (IAA^-) and H+ have low lipophilicity and permeability, and can only enter cells through AUX1/LAX influx carriers. In cells with strong alkalinity, IAA dissociates and needs to leave the cell through PIN or ABCB efflux transporter proteins. The polar localization of PIN protein determines the flow direction of auxin. Some intracellular IAA may be transported to the endoplasmic reticulum through PIN5, PIN6, and PIN8 to regulate the homeostasis and metabolism of auxin. PIN protein can be recovered by endocytosis and reinserted into lipid bilayer. The arrows indicate the direction of the auxin flow (refer to Robert et al., 2009 [36]; Friml et al., 2010 [37]; Wang et al., 2018 [38]).

3. Auxin Transport Carrier

3.1. Influx Carriers AUX1/LAX Family

The AUX1/LAX family encodes multimembrane-spanning transmembrane proteins, shares similarities with amino acid transporters (AAT), and forms a plant-specific subclass within the amino acid/auxin permease super family (AAAP) [39]. AAT is a family of transmembrane transporters, which is mainly responsible for the transport of amino acids and participates in the regulation of plant growth, development, metabolism, and responds to abiotic stress. There are many kinds of AAT families, including two major gene families: the AAAP family and aminoacid-polyamine-choline (APC) family [6,40,41]. There are four members of the *AUX1/LAX* family in the dicot model *Arabidopsis*, namely *AtAUX1*, *AtLAX1*, *AtLAX2*, and *AtLAX3*. *AtAUX1* (auxin resistant1) is the first auxin influx carrier cloned from *Arabidopsis thaliana*, which encodes an amino acid-like permease with 11 transmembrane structures [3,42]. The four genes encoding auxin influx carrier of*Arabidopsis* perform diverse biofunctions and evolve different regulatory mechanisms [3]. By homology comparison, five *AUX1-like* genes were found in monocotyledon rice, including *OsAUX1*, *OsAUX2*, *OsAUX3*, *OsAUX4*, and *OsAUX5*. The gene structure and protein structure of the rice *OsAUX* family were analyzed by bioinformatics. The results showed that *OsAUX1*, *OsAUX2*, *OsAUX3*, and *OsAUX4* all has 5–7 exons, *OsAUX5* has only 2 exons, while *AtAUX1/LAX* has 6–7 exons in *Arabidopsis thaliana*. The homology of its amino acid sequence ranged from 70.58% to 84.15%, and it was similar to the four proteins of *Arabidopsis thaliana*, indicating that the function of auxin influx carriers is conserved. It is predicted that the *OsAUX* family contains 9–11 transmembrane structures (Figure 3),

and the *OsAUX* family is putatively located on the cell membrane. To date, *OsAUX1*, *OsAUX3*, and *OsAUX4* have been reported, and were mainly involved in regulating root development and grain shape in our Lab [43–46].

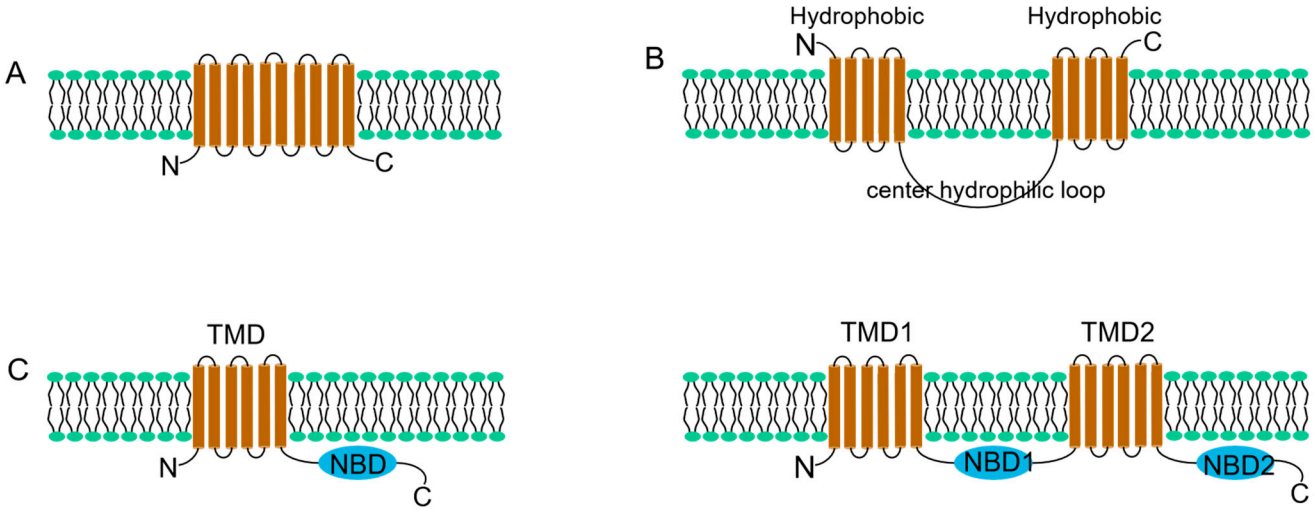

Figure 3. Structure model of protein. (**A**): Structure model of AUX protein. (**B**): Structure model of PIN protein. (**C**): Structure model of ABCB protein, Structural model of ABCB half-molecular transporter (**left**), Structural model of ABCB full-molecular transporter (**right**) (refer to Yu et al., 2015 [43]; Wang et al., 2008 [47]; Sánchez-Fernández et al., 2001 [48]).

3.2. Efflux Carrier PIN Family

The PIN family is the earliest studied auxin efflux carrier. The polar transport of auxin in plant tissues is largely at tributed to the highly regulated, polar-oriented PIN protein family [33,42,49]. *AtPIN1* is the first gene cloned in the *PIN* family, which shows developmental defects in inflorescences, forming needlelike inflorescences with almost no organs such as leaves and flowers on the stem, and weakening the ability of auxin transport from the base to the stem [50]. At present, 12 *PIN* genes have been reported in rice, including 4 *OsPIN1 (PIN1a-d)*, *OsPIN2*, *3*, *OsPIN5 (PIN5a-c)*, *OsPIN8*, *OsPIN9*, and 2 *OsPIN10 (PIN10a-b)* genes, among which *OsPIN9* and *OsPIN10* are unique to monocotyledons. However, *AtPIN3*, *AtPIN4*, *AtPIN6,* and *AtPIN7* in *Arabidopsis thaliana* were not found in rice genome. In terms of gene structure, *OsPIN* gene generally has 5–7 exons and 4–6 introns, while *AtPIN* gene generally has 6–7 exons and 4–6 introns [8,47]. In terms of protein structure (Figure 3), there is a major hydrophilic center separating the two hydrophobic regions, and each hydrophobic region has five transmembrane domains. Protein linkage analysis showed that OsPIN proteins were highly conserved in the two transmembrane regions. In the second hydrophobic region, there is a conserved structure of NPXXY, which is very important for the interaction between membrane protein and receptor protein in endocytosis, which also predicts the transmembrane transport function of rice PIN protein [47]. According to the length of the hydrophilic loop, PIN can be divided into two subfamilies, namely "long" PIN protein with a long hydrophilic loop and "short" PIN protein with a short hydrophilic loop. There are significant differences in the sequence variability of the hydrophobic domain between the two proteins, and they also have different localization and functions at the cellular level [51]. For example, in *Arabidopsis thaliana*, AtPIN1-AtPIN4 and AtPIN7 proteins have long hydrophilic loop polarity localization on cell membranes, mediating intercellular auxin transport; AtPIN5 and AtPIN8 have short hydrophilic loops located in the endoplasmic reticulum, and control the transport of auxin from the cell fluid to the endoplasmic reticulum cavity, thus regulating the stability and metabolism of auxin inside the cell. The hydrophilic loop of AtPIN6 lacks a conserved region compared to other "long" PIN proteins, so AtPIN6 can be localized to the plasma membrane and endoplasmic reticulum by phosphorylation [8,52–54]. In rice, "long" PIN proteins with long hydrophilic

loops are 4 OsPIN1(a–d) and OsPIN2, and "short" OsPIN proteins with short hydrophilic loops are 3 OsPIN5 (a–c) and OsPIN8, as well as three monocot specific PIN proteins (OsPIN9, OsPIN10a, OsPIN10b) [55–57]. In addition, OsPIN1, OsPIN2, OsPIN9, and OsPIN10a are located on the plasma membrane to determine the direction and speed of auxin transport [55,58–60]. OsPIN5b is located in endoplasmic reticulum to participate in auxin intracellular transport and balance [56]. OsPIN8 is similar to AtPIN8, which putatively located in endoplasmic reticulum like AtPIN8 [56].

3.3. Influx/Efflux Carriers ABCB Subfamily

The ATP binding Cassette (ABC) family is one of the largest known superfamilies in biology, widely existing in eukaryotic and prokaryotic organisms, including eight subfamilies of ABCA-ABCH [61]. ABC proteins play key roles in plant physiology and development [62,63]. In addition to eukaryotic ABC subfamilies A to G, the ABC family also has the ABCI subfamily with similar components to prokaryotic ABC multisubunit transporters in plants [61]. The ABC protein family plays an important role in facilitating the transport of different substrates, including hormones, pigments, toxic chemicals, and compounds related to reactive oxygen species (ROS) [64–67]. Plant hormones regulate the whole growth and development process of plants. Hormone transporters are crucial to the action of plant hormones, and some ABC families have been proved to mediate the transport of plant hormones [68–71]. For example, *OsABCG8* and *VviABCG14* transport cytokinins, respectively, in rice and *Vitis vinifera* [64,72]; *MtABCG20* affects root morphology and seed germination of *Medicago truncatula* through ABA transport [73]; *SlABCB4* is involved in auxin transport in fruit development in tomato [74]. ABCB is the second largest subfamily of ABC transporters after ABCG, involved in the polar transport of auxin [11]. The ABCB proteins have two domains (Figure 3): the conserved Nucleotide-binding domain (NBD) and lipophilic-helical transmembrane domain (TMD). NBD combines with ATP to release energy to activate substrates, and transmembrane transport via TMD [12]. According to the protein structure, ABC transporters can be divided into three categories: namely, whole molecule transporters, semimolecular transporters, and soluble transporters [48]. In general, whole molecular transporters are composed of two nucleotide binding domains and two transmembrane domains. Semimolecular transporters contain only one NBD domain and one TMD domain and perform a function by forming homodimer, heterodimer, or polymer. Soluble transporters NBD and TMD exist in different polypeptides [75]. Among them, ABCB subfamily proteins only have whole molecular transporters and semimolecular transporters. *AtPGP1* is the first gene cloned into the *ABCB* subfamily [76], and the polar auxin transport capacity of *atpgp1* mutants is reduced [77]. There are 27 *ABCB* genes in rice, namely *OsABCB1-OsABCB27*. The number of exons of these 27 genes ranged from 3 to 20; the number of exons of *AtABCB* also varies greatly [78]. The length and molecular weight of the encoding protein were widely distributed. Analysis of expression patterns showed that the expression of rice *ABCB* gene is tissue-specific, and the expression of this subfamily gene is significantly differentiated [78]. The prediction of subcellular localization of rice *ABCB* proteins showed that most *OsABCB* transporters are putatively located in plasma membrane, while *OsABCB3* is putatively located in vacuolar membrane and *OsABCB22* in cytoplasm [79].

4. The Biofunctions of Auxin Transporters in Rice

Polar auxin transport plays very important roles in regulating plant growth and development. The biological functions of some polar auxin transport carriers in rice have been successively revealed, which mainly function in regulating root growth and development, yield traits, plant architecture, and response to heavy metal stress (Table 1, Figure 4).

Table 1. Biological functions of auxin transporter in rice.

Gene	Biological Functions	Reference
OsAUX1	Root development Cadmium/low phosphorus stress response Gravitropism response	[43,80–82]
OsAUX3	Root development Grain length and grain weight Al stress response	[44,46]
OsAUX4	Root development Phosphate starvation response	[45]
OsPIN1	Root and shoot development Panicle formation/differentiation Regulation of negative Phototropism	[58,83–88]
OsPIN2	Root architecture Root elongation Lateral root formation Plant architecture	[59,89–91]
OsPIN5b	Plant architecture Yield	[56,92]
OsPIN9	Tiller Adventitious roots development	[60,93]
OsPIN10a(OsPIN3t)	Root development Drought stress response	[55]
OsABCB14	Mediates the acropetal transport of auxin Maintains iron balance	[94]
OsABCB23 (ATM3)	Iron and sulfur cluster assembly	[95]
OsABCB27(OsALS1)	Al stress response	[96]

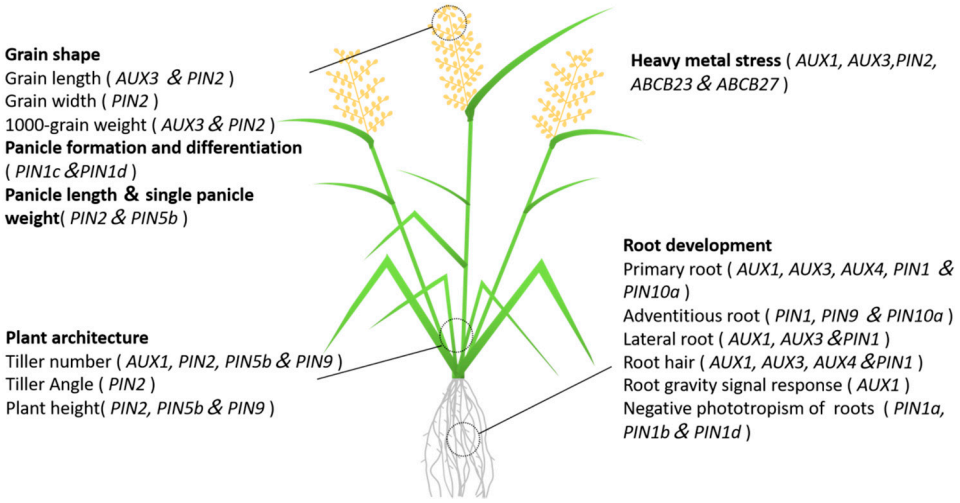

Figure 4. Roles of the *OsAUX*, *OsPIN*, and *OsABCB* family in rice development. Names in parenthesis indicate the genes controlling the respective role (refer to Yu et al., 2015 [43]; Wang et al., 2019 [44]; Ye et al., 2021 [45]; Qiao et al., 2021 [46]; Zhang et al., 2012 [55]; Wang et al., 2018 [59]; Hou et al., 2020 [60]; Zhao et al., 2015 [80]; Sun et al., 2021 [81]; Xu et al., 2013 [85], 2015 [87]; Hiroki et al., 2018 [89]; Wu et al., 2021 [93]; Xu et al., 2014 [94]; Liu et al., 2021 [88]; Zeng et al., 2019 [92]; Giri et al., 2018 [82]; Wu et al., 2014 [90], 2015 [91]; Feng et al., 2009 [96]; Zuo et al., 2017 [95]).

4.1. Auxin Transporters Is Involved in Root Development in Rice

Roots are an important plant organ and can anchor, absorb water and nutrients, synthesize and store nutrients, and maintain rhizosphere microorganisms. Developed roots play important roles in normal plant life activities and resistance to adverse environments. The growth and development of roots mainly include the growth of the primary root, lateral root, root hair, and adventitious root, which are related to many factors–among them, auxin

is one of the most important. The distribution and maintenance of auxin concentration gradient in plants depend on polar transport. Under normal culture conditions, the primary root of *osaux1* was longer than that of WT, and *OsAUX1* overexpression lines were shorter, indicating that *OsAUX1* negatively regulates the primary root of rice. The primary root of *osaux1* is insensitive to IAA, 2,4-D and sensitive to NAA, indicating that the mutation of *osaux1* destroys IAA and 2,4-D transport, but does not affect NAA influx [43]. 5-ethynyl-2′-deoxyuridine (EdU) assay showed that the activity of root apical meristem (RAM) was enhanced in *osaux1* lines, while the activity of RAM was reversed in overexpressed lines. In addition, a root length regulator 4, *OsRLR4,* binds to the *OsAUX1* promoter to negatively regulates RAM activity and regulate primary root elongation in rice [97]. Furthermore, studies have shown that *OsWOX4* (WUSCHEL-related homeobox) is a transcription factor of *OsAUX1* upstream and plays a role in primary root elongation by effecting auxin accumulation [98]. The root hair length of *osaux1* was shortened, and it could not be restored to WT after being treated with Indole-3-acetic acid (IAA) and 2, 4-dichlorophenoxyacetic acid (2, 4-D); however, naphthylacetic acid (NAA) could be restored to WT [43]. The lateral root density and length of *osaux1* seedlings were significantly reduced. In *osaux1* seedlings, auxin signaling pathway related genes *OsAIR1*, *OsIAA19,* and *OsIAA23*, and cell cycle related genes *OsCYCD4;1*, *OsCYCD5;2,* and *OsCDK2* were significantly down-regulated compared with WT, suggesting that *OsAUX1* promotes lateral root formation by influencing auxin signaling and cell cycle, and regulates root geotropism [80]. The primary root of *osaux3* mutant was shorter than that of the WT, the primary root of *OsAUX3* overexpressed lines was longer, and the primary root length of *osaux3*-complementary lines was similar to that of WT. The fluorescence intensity of EdU staining in primary root apex of *osaux3* mutants was decreased, while that of *OsAUX3* overexpressed lines was increased, indicating that *OsAUX3* is involved in primary root elongation of rice by altering cell division activity [44]. 2,3,5-triphenyltetrazolium chloride (TTC) staining results showed that the number of *osaux3* lateral root primordia was significantly reduced, while the overexpressed strain was significantly higher than the WT. The cell cycle-related genes *OsCYCD4;1*, *OsCYCB2;2*, *OsCYCU4;3*, *OsCDKC;1*, *OsCDKC;3*, and *OsCKL:10* expression are significantly down-regulated in *osaux3* mutants, which was contrary in overexpressed lines, revealing that *OsAUX3* regulates lateral root initiation by mediating the expression of these cell cycle-related genes [44]. Moreover, *OsAUX3* is also involved in aluminum-induced root growth inhibition [44]. The *osaux4* mutants have the character of shorter primary root, decrease in EdU staining and the expression down-regulation of genes related to cell division, demonstrating that *OsAUX4* altered the division of root apical meristem cells to participate in rice primary root growth [45]. *osaux4* mutants have longer root hair, showing that *OsAUX4* negatively regulates root hair development.

Studies have found that *OsPIN1* plays an important role in regulating the development of adventitious roots, tillering, and the proportion of underground and aboveground parts of rice, and down-regulating the expression of *OsPIN1* significantly inhibits tillering number and adventitious root occurrence of rice [83]. The seminal root of *ospin1b* mutant was shorter than WT, and the expression of *pCYCB1;1::GUS* in *ospin1b* was less affected by low nutrient conditions and SNP (sodium nitroprusside, NO donor) and GR24 (analogue of strigolactones) treatment, while the expression of *pCYCB1;1::GUS* in WT was significantly up-regulated, revealing that *OsPIN1b* plays a role in strigolactone and NO mediated seminal root elongation by influencing root tip meristem activity in response to low nitrogen and low phosphorus stress [81]. The expression levels of *OsAMT1;2* and *OsGDH2* in *ospin1b* mutants were significantly reduced in response to ammonium after long-term N-deficiency, indicating that *OsAMT1;2* and *OsGDH2* in the ammonium assimilation pathway can be regulated by *OsPIN1b* [99]. The double mutant of *ospin1a; pin1b* exhibited the reduction of adventitious roots and lateral roots, shorter primary roots, increased root hair density, loss of gravitropism, and dwarfed plant height, indicating that os*PIN1a* and os*PIN1b* are involved in root and shoot development [84]. The triple mutants *ospin1a; pin1b; pin1c* and *ospin1a; pin1b; pin1d* showed adventitious root loss and abnormal lateral

root development. The triple mutant *ospin1a; pin1b; pin1c* cannot initiate adventitious root primordial initiation and form adventitious root primordia, which leads to adventitious root loss [100]. The quadruple mutant *ospin1a; pin1b; pin1c; pin1d* showed abnormal phenotypes, such as absence of primary root and adventitious root, and severe gravitropism loss in aboveground parts. It was found that it could form radicle primordia during embryo formation. This indicates that the radicle cannot extend normally during seed germination, which leads to abnormal radicle development [100]. In addition, studies have shown that *OsPIN1a*, *OsPIN1b,* and *OsPIN1d* play roles in the regulation of negative phototropism in rice roots [85–87,101]. *OsPIN2* affects root gravitropism response and determines root architecture by regulating polar auxin transport in root tips [59]. In addition, *OsPIN2* participated in lateral root formation by regulating the auxin concentration in root tip [89]. The expression level of *OsPIN2* in rice under normal nutrient conditions was higher than under low phosphorus conditions. Under low phosphorus conditions, the development of lateral roots and root hairs of WT was similar to that of *OsPIN2* overexpression, suggesting that *OsPIN2* plays a key role in the growth and development of rice roots in response to low phosphorus stress. *OsPIN2* overexpression lines showed shorter seminal root length and lower auxin accumulation in the root cap, suggesting that *OsPIN2* might inhibit seminal root elongation by reducing auxin accumulation in the root cap. Under normal nutritional conditions, overexpression of *OsPIN2* increases auxin distribution in the root epidermis, resulting in greater root hair formation but less lateral root development [102]. The plant height of the *ospin9* mutant was significantly lower than that of WT, and the number of adventitious roots was significantly reduced [93]. It was found that the mutation of *OsPIN9* led to the up-regulation of the expression levels of *OsPIN1a* and *OsPIN5b*, suggesting that *OsPIN1a* and *OsPIN5b* may have a redundant relationship with *OsPIN9* and coregulate the root development in rice. The *OsPIN5a* expression was inhibited by the mutation of *OsPIN9*, suggesting that *OsPIN5a* and *OsPIN9* are likely to regulate plant growth and development in a mode of co-expression [93]. *OsPIN3t (OsPIN10a)* is involved in rice root development and plays a key role in vegetative growth. RNAi lines of *OsPIN3t* showed shorter primary roots, while the overexpression line of *OsPIN3t* resulted in longer primary roots and increased adventitious roots [55].

Moreover, compared with WT, the *osabcb14* mutant had longer shoots and primary roots, and decreased sensitivity to 2,4-D and IAA, but remained unchanged to NAA. Expression of the auxin early response genes *OsIAA3*, *OsIAA9*, *OsIAA23*, and *OsSAUR39* was significantly down-regulated in the *osabcb14* mutant shoots and roots, and the auxin concentration in the shoots and roots of *osabcb14* mutant was reduced, suggesting that *OsABCB14* plays a role in auxin transport in shoots or roots. Yeast expressing *OsABCB14* have a significantly higher capacity to absorb IAA than empty vector-transformed yeast. The *osabcb14* mutant had significantly higher IAA efflux than that of WT, while its IAA influx was significantly lower, suggesting that *OsABCB14* is involved in auxin influx. Acropetal auxin transport was decreased in *osabcb14* mutant roots and basipetal auxin transport was similar to WT, suggesting that *OsABCB14* mediated acropetal Auxin transport in the root [94].

4.2. Auxin Transporters Regulate Rice Yield Traits

Plant architecture is a critical factor to determine crop yield. The ideal rice plant architecture is thick stem, moderate plant height, compact plant architecture, less tillering, no ineffective tillering, large panicle, and more grains. Panicle number, grains per panicle, and 1000-grain weight are the three main factors of rice yield [103]; 1000-grain weight is mainly related to grain shape, which is mainly determined by grain length, width, thickness, and fullness [104]. The glume and endosperm development of rice seeds determine the grain shape. The proliferation and amplification of the glume cells limit grain development. The endosperm occupies most of the volume of mature seeds. Auxin regulates the development of glume and endosperm after fertilization, and is an important plant hormone that regulates seed development and affects rice yield [105]. The auxin

signaling pathway is normally mediated by auxin response factors (ARFs) that regulate auxin-responsive transcription in plants. ARFs are plant-specific B3-type transcription factors that bind specifically to the auxin response element (AuxRE), activating or repressing the auxin response genes. Recently, we reported that the miR167a-OsARF6-OsAUX3 pathway regulates grain length and weight by altering the volume of glume cells [46]. As a nuclear localization protein, *OsARF6* directly binds to the auxin response element of the promoter of *OsAUX3* gene and positively regulates *OsAUX3* expression. In addition, *miR167a* specifically binds to the *OsARF6* mRNA to inhibit its expression. Auxin reporter DR5:GUS staining and GUS activity assay showed that the distribution and content of auxin in glume cell growth were increased in *osarf6* and *osaux3* mutants. These results suggest that *OsARF6* and *OsAUX3* regulate rice grain length by altering the content and distribution of auxin in rice glume cells. The novel miR167a-OsARF6-OsAUX3 module provide potential new targets for improving rice yield. [46].

An overexpression of *OsLPA1* (Loose Plant Architecture) decreases the tiller angle and resistance to sheath blight disease by activating *OsPIN1a* in rice [106]. *OsPIN1c* and *OsPIN1d* were mainly expressed in young panicles and showed redundant function [88]. The double mutant of *ospin1cpin1d* is mainly characterized by bare acicular inflorescence similar to *atpin1* mutant, and significantly reduced the plant height and tillering number of plants. In addition, genes like *OsPID*, *OsLAX1*, *OsMADS1,* and *OsSPL14/IPA1*, which were key regulatory factors of reproductive development, were differently expressed in *ospin1c-1 ospin1d-1.* This indicates that *OsPIN1c* and *OsPIN1d* are involved in the formation and differentiation of panicles [84,88]. *OsPIN2* overexpression lines increased the tiller angle, tiller number, plant height, panicle length, panicle weight, grain length, grain width, and 1000-grain weight [107]. *OsPIN2* overexpression lines inhibited the expression of a gravitropism-related gene *OsLAZY1* in the shoots, but did not affect the expression of *OsPIN1b* and *OsTAC1,* which act as tiller angle controllers in rice. The data suggest that *OsPIN2*, together with *OsPIN1b* and *OsTAC1*, has a unique auxin-dependent regulation pathway that controls shoot architecture [108]. *OsPIN5b* is an endoplasmic reticulum localization protein involved in the dynamic balance, transport, and distribution of auxin in vivo. *OsPIN5b* overexpression lines had dwarfed plant height, fewer leaves and tillers, lower seed setting rate, shorter panicle length, and yield. On the contrary, the loss-function mutant of *OsPIN5b* showed an increase in tiller number, enhanced root activity, longer panicle, and higher yield [56,92]. The *ospin9* mutant exhibited a decrease in tiller number, while overexpression line was the opposite. The number of tillers and grain yield of *OsPIN9* overexpression lines was increased under low nitrogen conditions by field test [60]. The relative expression level of *OsPIN9* and fluorescence intensity of the *pOsPIN9: Ospin9-GFP* transgenic line significantly increased under NH_4^+ alone and mixed N form treatments than the control, while NO_3^- treatment did not. Compared with WT, the tiller numbers of the *ospin9* mutants were reduced when using only NH_4^+ or NO_3^-, while the tiller numbers of the *OsPIN9* overexpressed lines were different in response to the N form: the tiller number was increased only in the NH_4^+ condition, suggesting that NH_4^+ promoted the RNA and protein levels of *OsPIN9*. According to the morphological analysis of tiller buds in different leaves compared with WT treated with NO_3^-, WT induced by NH_4^+ mainly regulate the growth of tiller buds by affecting the elongation of tiller buds. Therefore, regulating the expression of *OsPIN9* can also affect rice tillering and reduce nitrogen fertiliser input [60].

4.3. Auxin Transporters Participate in Response to Heavy Metal Stresses

Heavy metal pollution has become a major threat to agricultural production, affecting plant metabolism, growth, and development. In 1998, Wu etc. pointed out that cadmium (Cd) and lead (Pb) could affect the growth and development of rice and reduce its yield [109]. Cadmium stress induced the expression of all five genes in the rice *OsAUX* family, especially *OsAUX1*. Under cadmium stress, *osaux1* mutants had shorter primary roots, severely reduced lateral roots, and almost no long root hair; the auxin content in roots decreased significantly [43]. Although the content of Cd in *osaux1* mutants did not

change, reactive oxygen-mediated damage was enhanced, which further enhanced the sensitivity of *osaux1* mutants to Cd stress. These results indicate that *OsAUX1* responds to Cd stress by changing auxin content in root [43]. Alternatively, *OsAUX1* is also involved in a low phosphorus stress response by promoting root hair elongation [82]. Under aluminum (Al) stress, the content of auxin in root tip, Al content, and damage mediated by aluminum-induced reactive oxygen species (ROS) of the *osaux3* mutant were slighter than those of WT, suggesting that *OsAUX3* was related with Al-mediated root growth inhibition [44]. Cd rapidly down-regulated the expression of the auxin efflux transporter genes *OsPIN1b*, *OsPIN1c,* and *OsPIN9* in the stele and lateral root primordium, resulting in the decrease in auxin accumulation to inhibit the whole process of rice lateral root development [110]. *OsPIN2* overexpression lines can alleviate the inhibition of Al on auxin transport in the base and alter the distribution of Al ions in root tip cells, as well as elevate endocytic vesicular trafficking and Al internalization, thus improving the tolerance of rice to Al [90,91]. *OsABCB27(OsALS1)*, a TAP (transporter associated with antigen processing) type transporter, is located on the vacuolar membrane and is involved in the Al stress response of rice [96]. *OsABCB23(ATM3)* is an ATM (ABC transporter of the mitochondria) type transporter, which locates on mitochondria and plays an important role in the assembly of iron (Fe) and sulfur clusters, suggesting that mitochondrial ATM3 transporter is crucial for Fe homeostasis in rice [95]. In addition, *OsABCB14* was also found to relate to Fe homeostasis [94]. The concentration of Fe ion in seed, shoot, and root in *osabcb14* mutants was significantly higher than that of WT. Under Fe deficiency condition, *osabcb14* mutants showed longer shoot and root, and the expression of the Fe deficiency-responsive genes, Fe-regulated transporter 1 (*IRT1*), *IRT2*, Fe-Responsive operator 2 (*IRO2279*), yellow-stripe like 15 (*YSL15*), nicotianamine aminotransferase 1 (*NAAT1*), natural resistance-associated macrophage protein 2 (*NRAMP2*), Nicotianamine synthase (*NAS1*), and *NAS2* were all up-regulated in *osabcb14* mutants, suggesting that the *osabcb14* mutant was insensitive to Fe deficiency, and *OsABCB14* might function in maintaining iron homeostasis.

5. Other Potential Auxin Transporter

In *Arabidopsis thaliana*, nitrate transporter NRT1.1 plays a crucial role in nitrate signal transduction and regulation of root growth, and has the ability to transport auxin [111]. Under effective low nitrogenous utilization conditions, NRT1.1 repressed the growth of lateral roots by promoting the outward transport of auxin. PIN-LIKES (PILS) is a novel auxin transporter that regulates auxin distribution in *Arabidopsis thaliana* cells. The protein PILS is highly similar to the PIN protein family in structure, and there are seven members in this family, namely, PILS1-PILS7 [112]. Studies have shown that PILS (1–3) and PILS (5–7) proteins locate on the endoplasmic reticulum and coordinate with PIN5 and PIN8 to regulate the concentration of auxin in cells. The *atpils2* and *atpils2pils5* double mutants showed increased hypocotyl length and lateral root density, while *AtPILS5* overexpression lines had a shorter hypocotyl length and decreased lateral root density compared to WT, suggesting that *AtPILS2* and *AtPILS5* showed functional redundancy in root development [112]. This is due to the deletion of the *AtPILS2* and *AtPILS5* gene, which affects intracellular auxin accumulation. Under normal culture conditions, *atpils6* mutants showed an increased overall organ growth, longer primary roots length, enlarged cotyledon area, and larger rosette leaves, whereas overexpressed plants did the opposite. This suggests that *AtPILS6* negatively regulates organ growth in *Arabidopsis thaliana* [113]. After 3 h of high temperature treatment, the fluorescence of PILS6-GFP decreased, indicating that high temperature affected the level of PILS6 protein. Stronger high temperature-induced auxin signal transduction was detected in the root tips of *atpils6* mutants compared with WT, showing that high temperature affects PILS6-dependent auxin signal transduction [113]. In rice, a total of seven rice *OsPILS* (PIN-like) genes were identified, including *OsPILS1*, *OsPILS2*, *OsPILS5*, two *OsPILS6 (OsPILS6a*, *OsPILS6b)*, and two *OsPILS7 (OsPILS7a*, *OsPILS7b)* [105]. The genomic organization of *OsPILS* genes reveals that *OsPILS1*, *OsPILS6a*, *OsPILS6b*, and *OsPILS7a* each contain 10 introns, *OsPILS5* has seven, *OsPILS7b* has nine, and *OsPILS2*

has one. Each PILS protein was predicted to have a central hydrophilic ring with five transmembrane domains on each side. All OsPILS proteins contains auxin carrier domain. According to the subcellular localization prediction results, *OsPILS2*, *OsPILS5*, *OsPILS6b*, and *OsPILS7a* are putatively located in the endoplasmic reticulum, *OsPILS1* and *OsPILS6a* are putatively located in vacuolar, while *OsPILS7b* is putatively located on the plasma membrane and in the endoplasmic reticulum [114]. Leaf and root tissues were treated with 5μM IAA, and all *OsPILS* genes were up-regulated in leaves and down-regulated in roots at the third week of development. The expression levels of *OsPILS* genes were different in different tissues and at different developmental stages under the treatment of exogenous auxin, indicating that they play a role in the regulation of auxin [114]. In addition, the vacuolar auxin transporter Walls Are Thin1 (WAT1) is a tonoplast-localized auxin transporter, playing a critical role for the vacuole in regulating intracellular auxin homoeostasis in plants [115]. WAT1 is a plant-specific protein that dictates secondary cell wall thickness of wood fibres and facilitates auxin export from isolated Arabidopsis vacuoles in yeast and in Xenopus oocytes. However, the biological functions of the above potential auxin transporters have not been investigated in rice.

6. Summary and Prospect

As one of the most important food crops in the world, rice supports more than half of the world's population. With the continuous growth of the world population, the shortage of various resources has gradually emerged, so improving crop yield and efficient scientific breeding has become a major challenge to the sustainable development of agriculture in this era. At present, the biological functions of key genes of rice agronomic traits have been gradually reported. Auxin is one of the important hormones in plant growth and development. Some comprehensive reviews have covered the role of auxin in rice growth and development. For example, Sara et al. explained in detail that auxin transporters play an important role in the development of monocotyledons [116]; Wang et al. provided new ideas for rice breeding and improvement by describing the effects of auxin synthesis, degradation, transportation, binding, and signal transduction on rice growth and development [38]; Swarup et al. summarized the role of the *AUX1/LAX* gene family on plant development and put forward new opinions on the establishment of the overall model of auxin transport [117]. This review focuses on how polar auxin transports play a role in rice growth and development and response to heavy metal stress. The research on auxin transports in rice is not only of great significance for the improvement of important agronomic characters of rice, but also helps to improve the regulation mechanism of polar auxin transport on rice growth and development.

The polar transport of auxin affects plant growth and development by affecting the distribution and content of auxin, and the AUX1/LAX, PIN, and ABCB protein families mediate the polar transport of auxin. In recent years, with the progress of genetics and molecular biology experimental methods, people have gained a better understanding on the mechanism of auxin transporter in plant growth and development. However, little is known about the functions of some carrier proteins, such as *OsAUX2*, *OsAUX5*, *OsPIN3*, *OsPIN4*, *OsPIN6-8,* and most *OsABCB* in rice. Studying the biological function of auxin transporter in rice growth and development will provide genetic resources for obtaining high yield and good quality rice through molecular design breeding, and contribute to the establishment of the overall model of auxin transport. Currently, the CRISPR-Cas9 gene editing technology has been widely used in rice; it can screen dominant traits, design and transform varieties, and improve yield and quality. CRISPR-Cas9 technology can better solve the problem of function redundancy of genes coding auxin transporters, and lay the foundation for accelerating the analysis of *OsAUX*, *OsPIN*, and *OsABCB* gene function. Auxin is transported by the above mentioned carriers, however, the understanding of how to coordinate the auxin transport between the various carriers and the specific transport process of auxin within the cell is limited. Furthermore, the carrier localization is very important for auxin transport direction and the mechanism and factor affecting carrier

localization need to be further studied. In addition, the biological functions of potential auxin transporters in rice should be explored further.

Author Contributions: Author Contributions: Conceptualization, Y.F., E.B. and Y.Q.; investigation, Y.F. and Y.Q.; review of technical concepts, Y.F., E.B. and Y.Q.; writing—review and editing, Y.F., E.B. and Y.Q.; funding acquisition, Y.Q. All authors have read and agreed to the published version of the manuscript.

Funding: This project was funded by grants from the National Natural Science Foundation of China (32060451), and the Zhejiang Provincial Natural Science Foundation of China (grant no. LZ19C020001).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Xu, Z. Polar transport of auxin and its role in the regulation of plant development. *Chin. Bull. Life Sci.* **1998**, *2*, 52–54.
2. Enders Tara, A.; Strader Lucia, C. Auxin activity: Past, present, and future. *Am. J. Bot* **2015**, *102*, 180–196. [CrossRef] [PubMed]
3. Yu, C.; Dong, W.; Zhang, C. Research progress of auxin transport carrier. *Agric. Sci. Yanbian Univ.* **2016**, *38*, 359–366.
4. Bennett, M.; Marchant, A.; Green, H.G.; May, S.T.; Ward, S.P.; Millner, P.A.; Walker, A.R.; Schulz, B.; Feldmann, K.A. Arabidopsis AUX1 Gene: A Permease-Like Regulator of Root Gravitropism. *Science* **1996**, *273*, 948–950. [CrossRef]
5. Swarup, R.; Friml, J.; Marchant, A.; Ljung, K.; Sandberg, G.; Palme, K.; Bennett, M. Localization of the auxin permease AUX1 suggests two functionally distinct hormone transport pathways operate in the Arabidopsis root apex. *Gene Dev.* **2001**, *15*, 2648–2653. [CrossRef]
6. Péret, B.; Swarup, K.; Ferguson, A.; Seth, M.; Yang, Y.; Dhondt, S.; James, N.; Casimiro, I.; Perry, P.; Syed, A.; et al. AUX/LAX Genes Encode a Family of Auxin Influx Transporters That Perform Distinct Functions during Arabidopsis Development. *Plant Cell* **2012**, *24*, 2874–2885. [CrossRef]
7. Swarup, R.; Péret, B. AUX/LAX family of auxin influx carriers—An overview. *Front Plant Sci.* **2012**, *3*, 225. [CrossRef]
8. Krecek, P.; Skůpa, P.; Libus, J.; Naramoto, S.; Tejos, R.; Friml, J.; Zažímalová, E. The PIN-FORMED (PIN) protein family of auxin transporters. *Genome Biol.* **2009**, *10*, 249. [CrossRef]
9. Zhou, J.J.; Luo, J. The PIN-FORMED auxin efflux carriers in plants. *Int. Mol. Sci.* **2018**, *19*, 2759. [CrossRef]
10. Lin, Y.; Qi, Y. Advances in Auxin Efflux Carrier PIN Proteins. *Chin. Bull Bot* **2021**, *56*, 151–165.
11. Geisler, M.; Aryal, B.; di Donato, M.; Hao, P. A critical view on ABC transporters and their interacting partners in auxin transport. *Plant Cell Physiol.* **2017**, *58*, 1601–1614. [CrossRef] [PubMed]
12. He, Z.; Li, D.; Qi, Y. Advances in biofunctions of the ABCB subfamily in plants. *Chin. Bull Bot* **2019**, *54*, 688–698.
13. Peer, W.A.; Blakeslee, J.J.; Yang, H.; Murphy, A.S. Seven things we think we know about auxin transport. *Mol. Plant* **2011**, *4*, 487–504. [CrossRef]
14. Blakeslee, J.J.; Peer, W.A.; Murphy, A.S. Auxin transport. *Curr. Opin. Plant Biol.* **2005**, *8*, 494–500. [CrossRef] [PubMed]
15. Lee, H.; Anindya, G.; Dongwook, L.R.; Minho, P.; Cho, H.-T. Intracellularly Localized PIN-FORMED8 Promotes Lateral Root Emergence in *Arabidopsis*. *Front. Plant Sci.* **2019**, *10*, 1808. [CrossRef]
16. Larsen, P.B.; Cancel, J.; Rounds, M.; Ochoa, V. *Arabidopsis ALS1* encodes a root tip and stele localized half type ABC transporter required for root growth in an aluminum toxic environment. *Planta* **2007**, *225*, 1447–1458. [CrossRef]
17. Swarup, K.; Benková, E.; Swarup, R.; Casimiro, I.; Péret, B.; Yang, Y.; Parry, G.; Nielsen, E.; De Smet, I.; Vanneste, S.; et al. The auxin influx carrier LAX3 promotes lateral root emergence. *Nat. Cell Biol.* **2008**, *10*, 946–954. [CrossRef]
18. Friml, J.; Benková, E.; Blilou, I.; Wisniewska, J.; Hamann, T.; Ljung, K.; Woody, S.; Sandberg, G.; Scheres, B.; Jürgens, G. Palme KAtPIN4 Mediates Sink-Driven Auxin Gradients and Root Patterning in Arabidopsis. *Cell* **2002**, *108*, 661–673. [CrossRef]
19. Kubeš, M.; Yang, H.B.; Richter, G.L.; Cheng, Y.; Młodzińska, E.; Wang, X.; Blakeslee, J.J.; Carraro, N.; Petrášek, J.; Zažímalová, E.; et al. The *Arabidopsis* concentration-dependent influx/efflux transporter ABCB4 regulates cellular auxin levels in the root epidermis. *Plant J.* **2012**, *69*, 640–654. [CrossRef]
20. Chang, L.; Xue, H. Advances in study of polar auxin transport. *J. Biol.* **2008**, *25*, 9–13.
21. Jiang, D.; Zhu, C.; Yang, L. *Plant Physiology*, 2nd ed.; Higher Education Press: Beijing, China, 2011; pp. 168–179.
22. Friml, J.; Palme, K. Polar auxin transport-Old questions and new concepts? *Plant Mol. Biol.* **2002**, *49*, 273–284. [CrossRef] [PubMed]
23. Jones, A.M. Auxin Transport: Down and Out and Up Again. *Science* **1998**, *282*, 2201–2203. [CrossRef] [PubMed]
24. Rashotte, A.M.; Brady, S.; Reed, R.; Ante, S.; Muday, G.K. Basipetal auxin transport is required for gravitropism in roots of Arabidopsis. *Plant Physiol.* **2000**, *122*, 481–490. [CrossRef] [PubMed]

25. Xu, Z.; Xue, H. *Plant Hormones: Function and Molecular Mechanism*; Shanghai Scientific & Technical Publishers: Shanghai, China, 2012; pp. 2–33.
26. Zou, F.; Wang, Q.; Zhou, J.; Ding, G. Auxin Regulating Plant Growth and Development: Research Progress. *Chin. Agric. Sci. Bull.* **2018**, *34*, 34–40.
27. Iino, M. Mediation of tropisms of lateral translocation of endogenous indole-3-acetic acid in maize coleoptiles. *Plant Cell Environ.* **1991**, *14*, 279–286. [CrossRef]
28. Trewavas, A. What remains of the Cholodny-Went theory? *Plant Cell Environ.* **1992**, *15*, 759–794.
29. Sang, D.; Chen, D.; Liu, G.; Liang, Y.; Huang, L.; Meng, X.; Chu, J.; Sun, X.; Dong, G.; Yuan, Y.; et al. Strigolactones regulate rice tiller angle by attenuating shoot gravitropism through inhibiting auxin biosynthesis. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 11199–11204. [CrossRef]
30. Rakusová, H.; Gallego-Bartolomé, J.; Vanstraelen, M.; Robert, H.S.; Alabadí, D.; Blázquez, M.A.; Benková, E.; Friml, J. Polarization of PIN3-dependent auxin transport for hypocotyl gravitropic response in Arabidopsis thaliana. *Plant J.* **2011**, *67*, 817–826. [CrossRef]
31. Li, X. The Effect of Phytohormones on Prostrate Growth and Key Genes Associated with Prostrate in Chrysanthemum. Ph.D. Thesis, Beijing Forestry University, Beijing, China, 2019; pp. 23–24.
32. Raven, J.A. Transport of indoleacetic acid in plant cell in relation to pH and electrical potential gradients, and its significance for polar IAA transport. *New Phytol.* **1975**, *74*, 163–172. [CrossRef]
33. Wisniewska, J.; Xu, J.; Seifertová, D.; Brewer, P.B.; Ruzicka, K.; Blilou, I.; Rouquié, D.; Benková, E.; Scheres, B.; Friml, J. Polar PIN Localization Directs Auxin Flow in Plants. *Science* **2006**, *312*, 883. [CrossRef]
34. Jürgen, K.-L.; Johannes, L.; Marta, Z.; Michael, S.; Lindy, A.; Christian, L.; Jirí, F. Differential degradation of PIN2 auxin efflux carrier by retromer-dependent vacuolar targeting. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 17812–17817.
35. Pan, J.; Ye, X.; Wang, C.; Tu, S. PIN2 -mediated polar auxin transport regulation of root gravitropism in *Arabidopsis thaliana*. *J. Zhejiang Norm. Univ. (Nat. Sci.)* **2010**, *33*, 1–6.
36. Robert, H.S.; Friml, J. Auxin and other signals on the move in plants. *Nat. Chem. Biol.* **2009**, *5*, 325–332. [CrossRef] [PubMed]
37. Friml, J. Subcellular trafficking of PIN auxin efflux carriers in auxin transport. *Eur. J. Cell Biol.* **2010**, *89*, 231–235. [CrossRef]
38. Wang, Y.; Zhang, T.; Wang, R.; Zhao, Y. Recent advances in auxin research in rice and their implications for crop improvement. *J. Exp. Bot* **2018**, *69*, 255–263. [CrossRef]
39. Young, G.B.; Jack, D.L.; Smith, D.W.; Saier, M.H., Jr. The amino acid/auxin:proton symport permease family. *Biochim. Biophys. Acta* **1999**, *1415*, 306–322. [CrossRef]
40. Ortiz-Lopez, A.; Chang, H.C.; Bush, D.R. Amino acid transporters in plants. *Bba-Biomembranes* **2000**, *1465*, 275–280. [CrossRef]
41. Zhao, H.; Ma, H.; Yu, L.; Wang, X.; Zhao, J. Genome-wide survey and expression analysis of amino acid transporter gene family in rice (*Oryza sativa* L.). *PLoS ONE* **2012**, *7*, e49210. [CrossRef]
42. Swarup, R.; Kargul, J.; Marchant, A.; Zadik, D.; Rahman, A.; Mills, R.; Yemm, A.; May, S.; Lorraine, W.; Millner, P.; et al. Structure-function analysis of the presumptive Arabidopsis auxin permease AUX1. *Plant Cell* **2004**, *16*, 3069–3083. [CrossRef]
43. Yu, C.; Sun, C.; Shen, C.; Wang, S.; Liu, F.; Liu, Y.; Chen, Y.; Li, C.; Qian, Q.; Aryal, B.; et al. The auxin transporter, OsAUX1, is involved in primary root and root hair elongation and in Cd stress responses in rice (*Oryza sativa* L.). *Plant. Cell Mol. Biol.* **2015**, *83*, 818–830. [CrossRef]
44. Wang, M.; Qiao, J.; Yu, C.; Chen, H.; Sun, C.; Huang, L.; Li, C.; Geisler, M.; Qian, Q.; Jiang, D.; et al. The auxin influx carrier, OsAUX3, regulates rice root development and responses to aluminium stress. *Plant Cell Environ.* **2019**, *42*, 1125–1138. [CrossRef] [PubMed]
45. Ye, R.; Wu, Y.; Gao, Z.; Chen, H.; Jia, L.; Li, D.; Li, X.; Qian, Q.; Qi, Y. Primary root and root hair development regulation by OsAUX4 and its participation in the phosphate starvation response. *J. Integr. Plant Biol.* **2021**, *63*, 1555–1567. [CrossRef] [PubMed]
46. Qiao, J.; Jiang, H.; Lin, Y.; Shang, L.; Wang, M.; Li, D.; Fu, X.; Geisler, M.; Qi, Y.; Gao, Z.; et al. A Novel miR167a-OsARF6-OsAUX3 Module Regulates Grain Length and Weight in Rice. *Mol. Plant* **2021**, *14*, 1683–1698. [CrossRef] [PubMed]
47. Wang, J. Preliminary Study of the Expression Patterns of *OsPINs*. Ph.D. Thesis, Zhejiang University, Hangzhou, China, 2008; p. 41.
48. Sánchez-Fernández, R.; Davies, T.G.E.; Coleman, J.O.D.; Rea, P.A. The *Arabidopsis thaliana* ABC protein superfamily, a complete inventory. *J. Biol. Chem.* **2001**, *276*, 30231–30244. [CrossRef]
49. Vieten, A.; Sauer, M.; Brewer, P.B.; Friml, J. Molecular and cellular aspects of auxin-transport-mediated development. *Trends Plant Sci.* **2007**, *12*, 160–168. [CrossRef]
50. Okada, K.; Ueda, J.; Komaki, M.K.; Bell, C.J.; Shimura, Y. Requirement of the polar auxin transport System in Early Stages of Arabidopsis Floral Bud Formation. *Plant Cell* **1991**, *3*, 677–684. [CrossRef]
51. Ganguly, A.; Park, M.; Kesawat, M.S.; Cho, H. Functional Analysis of the Hydrophilic Loop in Intracellular Trafficking of Arabidopsis PIN-FORMED Proteins. *Plant Cell* **2014**, *26*, 1570–1585. [CrossRef]
52. Jozef, M.; Petr, S.; Aurélien, B.; Klára, H.; Pavel, K.; Agnieszka, B.; Jan, P.; Jing, Z.; Vassilena, G.; York-Dieter, S.; et al. Subcellular homeostasis of phytohormone auxin is mediated by the ER-localized PIN5 transporter. *Nature* **2009**, *459*, 1136–1140.
53. Ding, Z.; Wang, B.; Moreno, I.; Duplakova, N.; Simon, S.; Carraro, N.; Reemmer, J.; Pěnčík, A.; Chen, X.; Tejos, R.; et al. ER-localized auxin transporter PIN8 regulates auxin homeostasis and male gametophyte development in Arabidopsis. *Nat. Commun.* **2012**, *3*, 941. [CrossRef]

54. Ditengou, F.A.; Gomes, D.; Nziengui, H.; Kochersperger, P.; Lasok, H.; Medeiros, V.; Paponov, I.A.; Nagy, S.K.; Nádai, T.V.; Mészáros, T.; et al. Characterization of auxin transporter PIN6 plasmamembrane targeting reveals a function for PIN6 in plant bolting. *New Phytol.* **2018**, *217*, 1610–1624. [CrossRef]
55. Zhang, Q.; Li, J.; Zhang, W.; Yan, S.; Wang, R.; Zhao, J.; Li, Y.; Qi, Z.; Sun, Z.; Zhu, Z. The putative auxin efflux carrier OsPIN3t is involved in the drought stress response and drought tolerance. *Plant J. Cell Mol. Biol.* **2012**, *72*, 805–816. [CrossRef] [PubMed]
56. Lu, G.; Coneva, V.; Casaretto, J.A.; Ying, S.; Mahmood, K.; Liu, F.; Nambara, E.; Bi, Y.-M.; Rothstein, S. OsPIN5b modulates rice (*Oryza sativa*) plant architecture and yield by changing auxin homeostasis, transport and distribution. *Plant J. Cell Mol. Biol.* **2015**, *83*, 913–925. [CrossRef] [PubMed]
57. Zhang, Y.; He, P.; Yang, Z.; Huang, G.; Wang, L.; Pang, C.; Xiao, H.; Zhao, P.; Yu, J.; Xiao, G. A Genome-Scale Analysis of the PIN Gene Family Reveals Its Functions in Cotton Fiber Development. *Front. Plant Sci.* **2017**, *8*, 461. [CrossRef]
58. Wu, L.; Han, L.; Zhao, Y.; Zhao, X.; Du, Y. Snbcellualar localization of auxin efflux carrier protein PIN1 in crop root and embryo. *Guihaia* **2021**, *41*, 1219–1225.
59. Wang, L.; Guo, M.; Li, Y.; Ruan, W.; Mo, X.; Wu, Z.; Sturrock, C.J.; Yu, H.; Lu, C.; Peng, J.; et al. LARGE ROOT ANGLE1, encoding OsPIN2, is involved in root system architecture in rice. *J. Exp. Bot* **2018**, *69*, 385–397. [CrossRef] [PubMed]
60. Hou, M.; Luo, F.; Wu, D.; Zhang, X.; Lou, M.; Shen, D.; Yan, M.; Mao, C.; Fan, X.; Xu, G.; et al. OsPIN9, an auxin efflux carrier, is required for the regulation of rice tiller bud outgrowth by ammonium. *New Phytol.* **2020**, *229*, 935–949. [CrossRef]
61. Verrier, P.J.; Bird, D.; Burla, B.; Dassa, E.; Forestier, C.; Geisler, M.; Klein, M.; Kolukisaoglu, J.; Lee, Y.; Martinoia, E.; et al. Plant ABC proteins–a unified nomenclature and updated inventory. *Trends Plant Sci.* **2008**, *13*, 151–159. [CrossRef]
62. Do Thanh, H.T.; Martinoia, E.; Lee, Y.; Hwang, J.-U. 2021 update on ATP-binding cassette (ABC) transporters: How they meet the needs of plants. *Plant Physiol.* **2021**, *187*, 1876–1892.
63. Do Thanh, H.T.; Martinoia, E.; Lee, Y. Functions of ABC transporters in plant growth and development. *Curr. Opin. Plant Biol.* **2018**, *41*, 32–38.
64. Zhao, J.; Yu, N.; Ju, M.; Fan, B.; Zhang, Y.; Zhu, E.; Zhang, M.; Zhang, K. ABC transporter OsABCG18 controls the shootward transport of cytokinins and grain yield in rice. *J. Exp. Bot.* **2019**, *70*, 6277–6291. [CrossRef]
65. Dean, G.C.; Paula, C.; Virginia, W. A multidrug resistance-associated protein involved in anthocyanin transport in Zea mays. *Plant Cell* **2004**, *16*, 1812–1826.
66. Song, W.-Y.; Yamaki, T.; Yamaji, N.; Ko, D.; Jung, K.-H.; Fujii-Kashino, M.; An, G.; Martinoia, E.; Lee, Y.; Ma, J.F. A rice ABC transporter, OsABCC1, reduces arsenic accumulation in the grain. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 15699–15704. [CrossRef] [PubMed]
67. Do Thanh, H.T.; Choi, H.; Palmgren, M.; Martinoia, E.; Hwang, J.-U.; Lee, Y. Arabidopsis ABCG28 is required for the apical accumulation of reactive oxygen species in growing pollen tubes. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 12540–12549.
68. Geisler, M.; Blakeslee, J.J.; Bouchard, R.; Lee, O.R.; Vincenzetti, V.; Bandyopadhyay, A.; Titapiwatanakun, B.; Peer, W.A.; Bailly, A.; Richards, E.L.; et al. Cellular efflux of auxin catalyzed by the Arabidopsis MDR/PGP transporter AtPGP1. *Plant J.* **2005**, *44*, 179–194. [CrossRef] [PubMed]
69. Feng, Y.; Sun, Q.; Zhang, G.; Wu, T.; Zhang, X.; Xu, X.; Han, Z.; Wang, Y. Genome-Wide Identification and Characterization of ABC Transporters in Nine Rosaceae Species Identifying MdABCG28 as a Possible Cytokinin Transporter linked to Dwarfing. *Int. J. Mol. Sci.* **2019**, *20*, 5783. [CrossRef]
70. Park, J.; Lee, Y.; Martinoia, E.; Geisler, M. Plant hormone transporters: What we know and what we would like to know. *BMC Biol.* **2017**, *15*, 93. [CrossRef]
71. Borghi, L.; Kang, J.; de Brito Francisco, R. Filling the Gap: Functional Clustering of ABC Proteins for the Investigation of Hormonal Transport in planta. *Front. Plant Sci.* **2019**, *10*, 422–440. [CrossRef]
72. Wang, L.; Xue, J.; Yan, J.; Liu, M.; Tang, Y.; Wang, Y.; Zhang, C. Expression and functional analysis of VviABCG14 from Vitis vinifera suggest the role in cytokinin transport and the interaction with VviABCG7. *Plant Physiol. Biochem.* **2020**, *153*, 1–10. [CrossRef]
73. Aleksandra, P.; Joanna, B.; Wanda, B.; Enrico, M.; Michał, J. MtABCG20 is an ABA exporter influencing root morphology and seed germination of Medicago truncatula. *Plant J.* **2019**, *98*, 511–523.
74. Ofori, P.A.; Geisler, M.; di Donato, M.; Pengchao, H.; Otagaki, S.; Matsumoto, S.; Shiratake, K. Tomato ATP-Binding Cassette Transporter SlABCB4 Is Involved in Auxin Transport in the Developing Fruit. *Plants* **2018**, *7*, 65. [CrossRef]
75. Wang, X.; Sun, Y.; Xiao, R.; Wu, X.; Li, Q.; Wang, B. Cloning and Expression Analysis of BnABCG8 Geng in Brassica napus. *Mol. Plant Breed* **2018**, *16*, 39–46. [CrossRef]
76. Dudler, R.; Hertig, C. Structure of an mdr-like gene from *Arabidopsis thaliana*. Evolutionary implications. *J. Biol. Chem.* **1992**, *267*, 5882–5888. [CrossRef]
77. Sidler, H.; Hasan, R.D. Involvement of an ABC transporter in a developmental pathway regulating hypocotyl cell elongation in the light. *Plant Cell* **1998**, *10*, 1623–1636. [CrossRef] [PubMed]
78. Xu, X.; Qiu, J.; Xu, Y.; Xu, C. Molecular Evolution and Expression Analysis of Subfamily ABCB Transporter Genes in Rice. *Chin. J. Rice Sci.* **2012**, *26*, 127–136.
79. Xu, Y. OsABCB14 Functions in Auxin Transport and Iron Homeostasis in Rice (*Oryza sativa* L.). Ph.D. Thesis, Zhejiang University, Hangzhou, China, 2014; p. 18.

80. Zhao, H.; Ma, T.; Wang, X.; Deng, Y.; Ma, H.; Zhang, R.; Zhao, J. OsAUX1 controls lateral root initiation in rice (*Oryza sativa* L.). *Plant Cell Environ.* **2015**, *38*, 2208–2222. [CrossRef]
81. Sun, H.; Tao, J.; Bi, Y.; Hou, M.; Lou, J.; Chen, X.; Zhang, X.; Luo, L.; Xie, X.; Yoneyama, K.; et al. OsPIN1b is Involved in Rice Seminal Root Elongation by Regulating Root Apical Meristem Activity in Response to Low Nitrogen and Phosphate. *Sci. Rep.* **2018**, *8*, 1–11. [CrossRef]
82. Giri, J.; Bhosale, R.; Huang, G.; Pandey, B.K.; Parker, H.; Zappala, S.; Yang, J.; Dievart, A.; Bureau, C.; Ljung, K.; et al. Rice auxin influx carrier OsAUX1 facilitates root hair elongation in response to low external phosphate. *Nat. Commun.* **2018**, *9*, 1408. [CrossRef]
83. Xu, M.; Zhu, L.; Shou, H.; Wu, P. A PIN1 Family Gene, OsPIN1, involved in Auxin-dependent Adventitious Root Emergence and Tillering in Rice. *Plant Cell Physiol.* **2005**, *46*, 1674–1681. [CrossRef]
84. Li, Y.; Zhu, J.; Wu, L.; Shao, Y.; Wu, Y.; Mao, C. Functional Divergence of PIN1 Paralogous Genes in Rice. *Plant Cell Physiol.* **2019**, *60*, 2720–2732. [CrossRef]
85. Xu, H.; Mo, Y.; Shi, G.; Jin, W.; Wang, Z. Preliminary Study on Function of OsPIN1a Gene in Negative Phototropism of Rice Roots. *Chin. J. Rice Sci.* **2013**, *27*, 466–472.
86. Xu, H.; Mo, Y.; Wang, W.; Wang, H.; Wang, Z. OsPIN1a Gene Participates in Regulating Negative Phototropism of Rice Roots. *Rice Sci.* **2014**, *21*, 83–89. [CrossRef]
87. Xu, H.; Wang, H.; Mo, Y. Construction and transformation of GFP fusion expression vector of rice OsPIN1b gene. *Guangdong Agric. Sci.* **2015**, *42*, 146–150.
88. Liu, J.; Shi, X.; Chang, Z.; Ding, Y.; Ding, C. Auxin Efflux Transporters OsPIN1c and OsPIN1d Function Redundantly in Regulating Rice (*Oryza sativa* L.) Panicle Development. *Plant Cell Physiol.* **2021**, *63*, 305–316. [CrossRef] [PubMed]
89. Hiroki, I.; Jahan, S.I.; Takaki, Y.; Shunsaku, N.; Misuzu, T.N.; Maya, M.; Atsushi, O.; Yusaku, N.; Yoshiaki, I. OsPIN2, which encodes a member of the auxin efflux carrier proteins, is involved in root elongation growth and lateral root formation patterns via the regulation of auxin distribution in rice. *Physiol. Plantarum.* **2018**, *164*, 216–225.
90. Wu, D.; Shen, H.; Yokawa, K.; Baluška, F. Alleviation of aluminium-induced cell rigidity by overexpression of OsPIN2 in rice roots. *J. Exp. Bot* **2014**, *65*, 5305–5315. [CrossRef]
91. Wu, D.; Shen, H.; Yokawa, K.; Baluška, F. Overexpressing OsPIN2 enhances aluminium internalization by elevating vesicular trafficking in rice root apex. *J. Exp. Bot* **2015**, *66*, 6791–6801. [CrossRef]
92. Zeng, Y.; Wen, J.; Zhao, W.; Wang, Q.; Huang, W. Rational Improvement of Rice Yield and Cold Tolerance by Editing the Three Genes OsPIN5b, GS3, and OsMYB30 with the CRISPR-Cas9 System. *Front Plant Sci.* **2019**, *10*, 1663. [CrossRef]
93. Wu, S.; Yang, X.; Zhang, Y.; Hou, D.; Xu, H. Generation of ospin9 Mutants in Rice by CRISPR/Cas9 Genome Editing Technology. *Sci. Agric. Sin.* **2021**, *54*, 3805–3817.
94. Xu, Y.; Zhang, S.; Guo, H.; Wang, S.; Xu, L.; Li, C.; Qian, Q.; Chen, F.; Geisler, M.; Qi, Y.; et al. OsABCB14 functions in auxin transport and iron homeostasis in rice (*Oryza sativa* L.). *Plant J. Cell Mol. Biol.* **2014**, *79*, 106–117. [CrossRef]
95. Zuo, J.; Wu, Z.; Li, Y.; Shen, Z.; Feng, X.; Zhang, M.; Ye, H. Mitochondrial ABC Transporter ATM3 Is Essential for Cytosolic Iron-Sulfur Cluster Assembly. *Plant Physiol.* **2017**, *173*, 2096–2109. [CrossRef]
96. Feng, H.C.; Naoki, Y.; Namiki, M.; Masahiro, Y.; Yoshiaki, N.; Feng, M.J. A bacterial-type ABC transporter is involved in aluminum tolerance in rice. *Plant Cell* **2009**, *21*, 655–667.
97. Sun, C.; Li, D.; Gao, Z.; Gao, L.; Shang, L.; Wang, M.; Qiao, J.; Ding, S.; Li, C.; Geisler, M.; et al. OsRLR4 binds to the OsAUX1 promoter to negatively regulate primary root development in rice. *J. Integr. Plant Biol.* **2021**, *64*, 118–134. [CrossRef] [PubMed]
98. Chen, R.; Xu, N.; Yu, B.; Wu, Q.; Li, X.; Wang, G.; Huang, J. The WUSCHEL-related homeobox transcription factor OsWOX4 controls the primary root elongation by activating OsAUX1 in rice. *Plant Sci.* **2020**, *298*, 110575. [CrossRef]
99. Gho, Y.; Song, M.Y.; Bae, D.Y.; Choi, H.; Jung, K. Rice PIN Auxin Efflux Carriers Modulate the Nitrogen Response in a Changing Nitrogen Growth Environment. *Int. J. Mol. Sci.* **2021**, *22*, 3243. [CrossRef]
100. Wu, L. Effect of OsPIN1 Paralogous Genes on the Development of Rice Root System. Ph.D. Thesis, Zhejiang University, Hangzhou, China, 2021; pp. 22–26.
101. Liang, G.; Xu, H.; Fang, Q.; Mo, Y. *OsPIN*1d Gene Clone and Its Function Analysis in Negative Phototropism of Rice Roots. *Acta Bot Boreal. Occident Sin.* **2017**, *37*, 1896–1903.
102. Sun, H.; Guo, X.; Xu, F.; Wu, D.; Zhang, X.; Lou, M.; Luo, F.; Xu, G.; Zhang, Y. Overexpression of OsPIN2 Regulates Root Growth and Formation in Response to Phosphate Deficiency in Rice. *Int. J. Mol. Sci.* **2019**, *20*, 5144. [CrossRef]
103. Zhang, J.; Huang, C.; Wang, H.; Huang, M.; Guo, T.; Xiao, W.; Chen, Z.; Liu, Y. Correlation and path analysis of single plant yield-related traits of rice. *Jiangsu Acad. Agric. Sci.* **2019**, *47*, 108–113.
104. Xing, Y.; Zhang, Q. Genetic and Molecular Bases of Rice Yield. *Annu. Rev. Plant Biol.* **2010**, *61*, 421–442. [CrossRef]
105. Jia, L.; Qi, Y. Advances in the Regulation of Rice (*Oryza sativa*) Grain Shape by Auxin Metabolism, Transport and Signal. *Chin. Bull. Bot.* **2022**, *57*, 1–12.
106. Qian, S.; Ya, L.T.; Dan, L.D.; Yuan, W.Z.; Shuang, L.; Pin, L.D.; Xiao, H.; Miao, L.J.; Hu, X.Y. Overexpression of Loose Plant Architecture 1 increases planting density and resistance to sheath blight disease via activation of PIN-FORMED 1a in rice. *Plant Biotechnol. J.* **2019**, *17*, 855–857.
107. Chen, Y. Regulatory Effect of OsPIN2, a Putative Auxin Efflux Transporter, on Rice Architecture, Root Morphology and Phosphorus Nutrition. Ph.D. Thesis, Nanjing Agricultural University, Nanjing, China, 2012; pp. 56–61.

108. Chen, Y.; Fan, X.; Song, W.; Zhang, Y.; Xu, G. Over-expression of OsPIN2 leads to increased tiller numbers, angle and shorter plant height through suppression of OsLAZY1. *Plant Biotechnol. J.* **2012**, *10*, 139–149. [CrossRef] [PubMed]
109. Wu, Y.; Yu, G.; Wang, X.; Liang, R. Compound Pollution of Cd, Pb, Cu, Zn and As on Lowland Rice. *Agro-Environ. Prot.* **1998**, *17*, 49–54.
110. Wang, H.; Xuan, W.; Huang, X.; Mao, C.; Zhao, F. Cadmium inhibits lateral root emergence in rice by disrupting OsPIN-mediated auxin distribution and the protective effect of OsHMA3. *Plant Cell Physiol.* **2021**, *62*, 166–177. [CrossRef]
111. Krouk, G.; Lacombe, B.; Bielach, A.; Perrine-Walker, F.; Malinska, K.; Mounier, E.; Hoyerova, K.; Tillard, P.; Leon, S.; Ljung, K.; et al. Nitrate-Regulated Auxin Transport by NRT1.1 Defines a Mechanism for Nutrient Sensing in Plants. *Dev. Cell* **2010**, *18*, 927–937. [CrossRef] [PubMed]
112. Barbez, E.; Kubeš, M.; Rolčík, J.; Béziat, C.; Pěnčík, A.; Wang, B.; Rosquete, M.R.; Zhu, J.; Dobrev, P.I.; Lee, Y.; et al. A novel putative auxin carrier family regulates intracellular auxin homeostasis in plants. *Nature* **2012**, *485*, 119–122. [CrossRef]
113. Elena, F.; Feraru, M.I.; Elke, B.; Sascha, W.; Lin, S.; Angelika, G.; Jürgen, K.-V. PILS6 is a temperature-sensitive regulator of nuclear auxin input and organ growth in Arabidopsis thaliana. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 3893–3898.
114. Tapan, M.; Nibedita, M.; Hanhong, B. Identification and Expression Analysis of PIN-Like (PILS) Gene Family of Rice Treated with Auxin and Cytokinin. *Genes* **2015**, *6*, 622–640.
115. Philippe, R.; Oana, D.; Réka, N.; Judith, F.; Claire, C.; Ondřej, N.; Kris, M.; Benoît, L.; Yves, M.; Stephanie, P.; et al. Arabidopsis WAT1 is a vacuolar auxin transport facilitator required for auxin homoeostasis. *Nat. Commun.* **2013**, *4*, 2625.
116. Sara, B.; Gurmukh, S.J.; Nicola, C. The role of auxin transporters in monocots development. *Front. Plant Sci.* **2014**, *5*, 393.
117. Swarup, R.; Bhosale, R. Developmental Roles of AUX1/LAX Auxin Influx Carriers in Plants. *Front. Plant Sci.* **2019**, *10*, 1306. [CrossRef]