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How to cite

ROBE, Kevin, BARBERON, Marie. Nutrient carriers at the heart of plant nutrition and sensing. In: Current opinion in plant biology, 2023, vol. 74, p. 1–10. doi: 10.1016/j.pbi.2023.102376

This publication URL:https://archive-ouverte.unige.ch/unige:169113Publication DOI:10.1016/j.pbi.2023.102376

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Nutrient carriers at the heart of plant nutrition and sensing



Kevin Robe and Marie Barberon

Abstract

Plants require water and several essential nutrients for their development. The radial transport of nutrients from the soil to the root vasculature is achieved through a combination of three different pathways: apoplastic, symplastic, and transcellular. A common feature for these pathways is the requirement of carriers to transport nutrients across the plasma membrane. An efficient transport of nutrients across the root cell layers relies on a large number of carriers, each of them having their own substrate specificity, tissular and subcellular localization. Polarity is also emerging as a major feature allowing their function. Recent advances on radial transport of nutrients, especially carrier mediated nutrient transport will be discussed in this review, as well as the role of transporters as nutrient sensors.

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Current Opinion in Plant Biology 2023, 74:102376

This review comes from a themed issue on Cell Biology and Cell signaling 2023

Edited by Bert De Rybel and Juan Dong

For a complete overview see the Issue and the Editorial

Available online xxx

https://doi.org/10.1016/j.pbi.2023.102376

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Keywords

Root, Nutrient, Transporter, Channel, Transceptor.

Introduction

Plants require water and at least 14 essential minerals for their development. To meet their nutritional needs, plant roots explore the soil to constantly reach new nutrient-rich zones. Nutrient uptake can occur at the root tip (for certain nutrients) as well as in differentiated roots where the epidermis with its root hairs plays the role of surface of absorption. In differentiated roots, nutrients are transported radially from the root periphery to the central vasculature, where they are loaded into the xylem and then transported to the leaves and sink tissues. On their way to the xylem vessels, nutrients can diffuse into the extracellular space between the cells until they are blocked in differentiated roots by Casparian strips (CS) at the endodermis (apoplastic pathway) (Figure 1a). The presence of CS force water and nutrients to enter the symplast (the latest at the endodermal level), prior reaching the vasculature. After their uptake by a cell (at the root cap, epidermal, cortical or endodermal levels), nutrients can theoretically be subsequently transported from cell to cell through plasmodesmata (cytoplasmic connections between adjacent cells) before their efflux into the xylem (symplastic pathway). A last possibility would be a transport mediated by polarized influx and efflux carriers along the root cell layers (coupled transcellular pathway). This latter pathway is predicted to be barred by suberin lamellae (second stage of endodermal differentiation) deposited at the periphery of endodermal cells (Figure 1b) [1]. A common feature of these three pathways is the requirement of an uptake by a membrane-located nutrient carrier. Several decades of research on mineral nutrition have seen the identification and characterization of dozens of nutrient carriers in plants (Table 1). However, the carrier-mediated nutrient transport is still poorly understood, mainly due to incomplete information on carriers' localization in vivo for many of them. In this review, we discuss recent advances of plant mineral nutrition in the context of the carrier-mediated radial transport of nutrients. The importance of carrier localization and polarity for their function will be highlighted as well as the role of some carriers as nutrient sensors.

Three different pathways but one common point: The need of nutrient carriers

Minerals move radially through the different root cell layers (epidermis, exodermis in some species, cortex, endodermis, and pericycle) via a combination of three but not mutually exclusive pathways: apoplastic, symplastic, and coupled transcellular whose contribution changes along the gradient of root differentiation (Figure 1c). The apoplastic pathway favors cations diffusion in the apoplast as the negative charges of the cell wall pectin would repel anions [2]. Recent studies on rice, tomato, and *Brassica rapa* unraveled the importance of this pathway in these species, although strong





Theoretical pathways for radial transport of nutrients in Arabidopsis root (transversal view). (a) Schematic representation of nutrients radial transport in Arabidopsis root after CS establishment (state I endodermis differentiation). The apoplastic pathway is blocked by the CS at the endodermis. (b) Schematic representation of nutrients radial transport in Arabidopsis root after CS establishment and suberin lamellae deposition (state II endodermis differentiation). The suberin lamellae deposition (state II endodermis differentiation). The suberin lamellae deposition (state II endodermis differentiation). The suberin lamellae blocks the diffusion into the endodermal symplast and is predicted to block the transcellular pathway. (c) The combination and interconnexion of the three pathways along the root cell layers allow an efficient radial transport of nutrients in the root. The transcellular pathway is facilitated by polarized influx and efflux carriers. The chemical properties of the nutrients, the physiology of the plant and the root development stage influence the pathway of nutrient transport.

discrepancies exist. Ca^{2+} , Na^+ , and Mg^{2+} are among the most common cations overaccumulated in CS mutants in comparison to wild type (WT) plants, similarly to what mutant analysis suggested in Arabidopsis thaliana $[3,4,5\bullet,6\bullet,7\bullet\bullet]$. On the other hand, several cations such as K^+ , Fe^{2+} , Zn^{2+} , Mn^{2+} , Si^{2+} , or Mo^{2+} were shown to be less accumulated in many CS mutants, emphasizing the dual role of CS in preventing both uncontrolled uptake of nutrients and leakage from the stele. Raman imaging of water recently re-enforce this latest role by demonstrating that H₂O does not diffuse from the stele to the cortex when CS are functional [8••]. Interestingly, the importance of CS integrity in nutrient carriers' accumulation at the endodermal level was recently pointed out in rice [7••] where lower silicon and manganese accumulation in the CS mutant oscaps1 (Casparian strip membrane domain protein 1), correlated to a reduced abundance of OsLsi1 (low-silicon rice 1) and OsNRAMP5 (natural resistance-associated macrophage protein 5), respectively. However, how CS defects lead to reduced nutrient carriers' abundance is still to be clarified. One appealing hypothesis would be that, similarly to the inactivation of aquaporins through CIFs/SGN3 (CS integrity factors/SCHENGEN3) signaling pathway in the CS mutant *esb1* [9], CS defects in oscasp1 could be sense by CIFs/SGN3 and subsequently lead to reduced nutrient carriers' accumulation. Interestingly, this pathway was also reported to modulate the developmental program of CS formation in response to low K^+ availability [10••].

The apoplast is often seen as a storage compartment, where minerals only diffuse upon their ionic gradients. Interestingly, it was recently shown that Fe dependent galactosylation of side chain A on rhamnogalacturonan-II promote Fe release from the cell wall, and thus allow uptake into the symplast [11•]. This could suggest that under specific nutrient deficiency, the cell wall composition and structure can be modified to increase the availability of some elements. Considering the number of cations that can be stored in the apoplast investigating how plants can remobilize them under specific conditions deserves much more attention [2,12,13].

While a purely apoplastic transport can only occur before CS formation (*i.e.*, in the root tip and elongation zone), the latter two pathways (symplastic and coupled transcellular) require ions to cross plasma membranes at least twice (Figure 1b) through influx and efflux carriers. Ions need to enter the symplast in either the epidermis, cortex or endodermis through an influx carrier before their export to the xylem apoplast [14]. In the symplastic pathway, ions diffuse from cell to cell through plasmodesmata (PD). Evidence of a contribution of plasmodesmata in nutrient radial transport are scarce. The ER (endoplasmic reticulum) localization of

AtMTP2 (metal-tolerance protein 2) suggest that Zn transport might occur inside the ER-luminal continuum through the desmotubules of plasmodesmata. This is supported by a significantly lower shoot Zn partitioning in *mtp2* than in the WT upon growth on Zn-deficient medium [15]. The presence of several nutrient carriers at the ER could mean that the ER-luminal continuum through the PD plays roles in symplastic nutrient transport [16–18]. The coupled transcellular pathway differs from the symplastic pathway with the contribution of polarized influx and efflux carriers in the same cell (Figure 1b). This pathway was clearly shown for the transport of Mn, Si, and B through the exodermal and endodermal transporters OsMTP9/OsNRAMP5, OsLsi1/OsLsi2 and AtNIP5.1/AtBOR1 respectively [19]. The transcellular pathway is supposed to be barred by the suberin lamellae, already shown to block the diffusion from the apoplast to the endodermal symplast [20]. Preventing uncontrolled diffusion into the endodermal symplast might be relevant for specific elements such as Ca²⁺ or boric acid, known to diffuse across lipidic layer $[21 \bullet , 22]$. The precise role of endodermal suberization on endodermal carriers (accumulation and function) remains to be determined and could possibly add another function to the deposition of suberin.

How the three pathways are coordinated in the root as well as the relative contribution of each pathway for individual nutrients transport remains poorly understood. It was recently clarified for ammonium (NH_4^+) transport $[23 \bullet \bullet]$. While the symplastic pathway was shown to dominate the radial movement of NH₄⁺ across root layers with the epidermal AMT1.3 (ammonium transporter 1.3) transporter in low ammonium conditions, the apoplastic pathway prevailed in high ammonium conditions with the cortical and endodermal AMT1.2 transporter (ammonium transporter 1.2). It is noteworthy that such studies remain the exception in the field and the contribution of each pathway for the other nutrients remain elusive. This highlights, if necessary, the highly complex route of carrier-mediated nutrient transport in the root and the importance to have nutrient carriers in different cell layers.

Getting into the cells, why do carriers' localization and polarity matter?

The distribution of carriers in the different cell layers of the root and at different subcellular levels is critical to allow the proper uptake of nutrients and coordination of the different pathways for nutrient transport. Their identification and localization started several decades ago but many are still unknown or uncharacterized. For many carriers, protein localization was initially investigated in heterologous systems where functionality and polarity could not be addressed. A tentative overview of nutrient carriers for which in planta localization with functional fusion or immunolocalization were investigated is presented in Table 1. In term of localization,

most are predicted to be at the PM, where they are expected to mediate nutrient uptake. This was demonstrated for phosphate, where the uptake is severely compromised when AtPHT1 (phosphate transporter 1) transporters are not targeted to the PM in absence of AtPHF1 (phosphate transporter traffic facilitator1) [24,25]. As briefly mentioned in the previous section, the localization of carriers not only at the PM but in a polar fashion should play a key role in the radial transport through the transcellular pathway as well as for the entry and exit points in the other pathways (Figure 1c) [26]. The polar localization to the outer or inner PM domains (facing the outer soil or the inner vasculature respectively) of nutrient carriers has been reported for a subset of them (Table 1) and their polarity was shown for several of them to play a key role for their function. For instance, disrupting AtNIP5; 1, AtBOR1 and AtBOR2 (Nod26-like intrinsic protein 5; 1, requires high boron 1, requires high boron 2, respectively) polarity by preventing their AP-2-dependent clathrin mediated endocytosis leads to a higher susceptibility to boron deficiency [27,28•]. Consequently, ap2m mutants showed more severe growth reduction when grown under low B conditions compare to WT. Similarly, polarity of OsLsi1 is required for efficient uptake of Si [29]. Another case is the outer polar localization of the metal influx transporter AtIRT1 (iron-regulated transporter 1) where apolar localization leads to exacerbated iron deficiency, re-emphasizing the crucial role of carrier polarity for plant nutrition [30,31]. Despite the importance of AtNRAMP1 (natural resistance-associated macrophage protein 1) in Mn nutrition, the role of its polarity has not yet been investigated [32,33]. However, the PM stabilized/non phosphorylable AtNRAMP1S20,22,24A version displays Mn toxicity symptoms, similarly to the PM stabilized IRT1 [34]. Even though the mechanisms responsible for nutrient carriers' polarization are known for some specific case, it cannot be generalized to all polar carriers. Suggesting that cell specific cues control polarity, OsLsi3, non-polar in the pericycle, showed inner polarization when expressed in the exodermis and endodermis. Importantly, polarity to the outer domain of influx carriers is not restricted to the differentiated root. Hence, B uptake in Brassica napus was shown to occur mainly in the root tip via the polarly localized BnaA3.-NIP5;1 transporter [35]. Considering for example that 20% of the total Pi uptake occurs in the root cap [36] and that B accumulates primarily in root tip in Arabidopsis [37], we can predict that more polarly localized carriers involved in the uptake of nutrients at the root cap will be identified.

For an efficient uptake and transport of mineral elements, a co-operative system mediated by both influx and efflux carriers localized in different root cell layers and possibly polarized is required. To date, the best examples of transcellular transport in the root are the

Species	Carrier	Substrates	Protein localization ^a	Tissue localization						Reference
				Ep	Hyp/Exo	Co	End	Pe	Vasc	
Arabidopsis thaliana	AtAMT1; 1	NH_4^+	PM, apolar			\checkmark				[72]
	AtAMT1; 2	NH ₄ ⁺	PM, apolar	·		, V	\checkmark			[73]
	AtAMT1; 3	NH ₄ ⁺	PM, apolar	\checkmark		V				[23]
	AtIRT1	Fe ²⁺ , Mn ²⁺ , Ni ²⁺ , Co ²⁺ , Zn ²⁺ , cd ²⁺	PM, outer polarity	V					\checkmark	[30,31]
	AtNIP5; 1	B(OH) ₃	PM, outer polarity	, V						[27]
	AtNIP6.1	B(OH) ₃	PM, outer polarity	V						[27]
	AtBOR1	B(OH) ₄ -	PM, inner polarity	, V			\checkmark			[28]
	AtBOR2	B(OH) ₄	PM, inner polarity	م			•			[74]
	AtBOR4	B(OH) ₄	PM, outer polarity	J						[75]
	AtNRT1.1	NO ₃ , auxin	PM, ?	J						[58]
	AtNRT2.1	NO3	PM, ?	J						[76]
	AtNRT2.4	NO ₃ -	PM, outer polarity	J		•				77
	AtNRAMP1	Fe^{2+} . Mn ²⁺	PM, outer polarity	Ĵ		1			1	[33]
	AtPHO1	Pi	intracellular, apolar	v		v		1	v	[78]
	AtPHT1.1	Pi	PM. ?					•		[25]
	AtHMA2	Zn ²⁺ Cd ²⁺ , Pb ²⁺ , Ni ²⁺ , Co ²⁺ , Cu ²⁺	PM. ?	•		· ·		1		[79]
	AtHMA4	Zn ²⁺ Cd ²⁺	PM, apolar					Ĵ		[80]
	AtCHX21	Na ⁺	PM ?				1	v		[81]
	AtSULTB2: 1	SO4 ²⁻	PM ?	1		./	2		1	[82]
Noccaea caerulescens	NcNramp1	Cd ²⁺	PM apolar	v		v		./	Ň	[83]
Oriza sativa	OsNramp5	Mn ²⁺	PM outer polarity		./		Ň	v	v	[84]
onza odilva	Osl si1	B(OH) ₂ Si(OH) ₄	PM outer polarity		N N		Ň			[85]
	Osl si2	Si(OH)₄	PM inner polarity		N N		Ň			[86]
	Osl si3	Si(OH)	PM apolar		v		v	./		[87]
		Si(OH)	PM outer polarity	./	./	./	./	Ň,	1	[88]
		Zn ²⁺	PM apolar	Ň	N /	Ň	Ň	Ň	Ň	[80]
		B(OH). ⁻	PM inner polarity	Ň	N /	Ň	Ň	Ň	Ň	[85]
		ын +	PM outer polarity	v	N /	v	v	v	N /	[00]
	$O_{\rm C}$ (MT1: 2	NH .+	PM outer polarity		N /				V	[90]
	$O_{c}AMT1; 2$	NH .+	PM outer polarity		N /					[90]
	OcMTPO	Mn +	PM inport polarity		N /		1			[90]
		7 n ⁺	PM apolar		V		V	1		[91]
			PM outer polarity	1	1	1	1	N,	1	[92]
	OSNIPS, I	$D(U\Pi)_3$ $Cd^{2+} Mp^{2+}$	PM, onder	V,	V /	N,	N,	V,	\checkmark	[93]
Brazziaz poppus			Pivi, apolar	V,	V	V	V	\checkmark		[94]
	DHAAS.NIFS, I		PM, outer polarity	V						[35]
Hordeum vulgarum	HVYSI		PM, apolar	\checkmark			1			[95]
	HVYSL2	Ni(II)–DMA, Zn(II)–DMA, Ni(II)–DMA, Cu(II)–DMA, Mn(II)–DMA, Co(II)–DMA	Рм, ароаг				V			[90]
	HvLsi6	Si(OH) ₄	PM, outer polarity	\checkmark	\checkmark	\checkmark	\checkmark			[97]
	HvLsi2	Si(OH)₄	PM, apolar				V			[98]
	HvLsi1	Si(OH)₄	PM, outer polarity		\checkmark		V			[99]
	HvNramp5	$Cd^{2+} Mn^{2+}$	PM, apolar		·		v			[100]
Cucumis sativus	Csl si1	Si(OH)	PM outer polarity in End	•		1	1		•	[101]



AtBOR1/AtNIP5:1 system for B transcellular transport, the OsLsi1/OsLsi2 for Si transcellular transport and OsNramp5/OsMTP9 for Mn transcellular transport [19,38,39]. For most nutrients however, a co-operative system of influx and efflux carriers has not yet been clearly identified, although predicted to be present at least for the release to xvlem vessels. For example, while Fe and Zn uptake is mainly mediated by the influx transporter AtIRT1 in the root epidermis with contribution from the vasculature, Fe efflux transporters are still not described [40,41•,42]. Several ZIP (ZRT, IRT-like proteins), able to transport Fe and expressed in the stele could be candidates, such as AtIRT3 (Iron Regulated Transporter 3) [43,44]. Recently, four PM redundant stele-expressed ZIP transporters (AtZIP4/AtZIP6/AtZIP9/AtIRT3) were shown to be involved in Zn translocation from root to shoot, making them good candidates for Zn efflux transporters [45].

Intriguingly, several nutrient carriers such as AtNRAMP6 (natural resistance-associated macrophage protein 6) or AtPHO1 (Phosphate 1), localize at the Golgi/trans Golgi network [46,47]. This questions how transporters located in the endomembrane system can mediate nutrient transport in the plant. One possibility would be that these transporters localize at the PM in specific conditions or in a very transient way as it was described for AtIRT1 [30,48-50] Another possibility could be that intracellular nutrient carriers allow the loading of minerals into secretory vesicles, which would subsequently be secreted to the apoplast. This last possibility was recently highlighted by a study where two NPF (NRT1/PRT Family) were shown to load nicotianamine (a metal chelator) into secretory vesicles $[51 \bullet \bullet]$.

Plant transceptors, exception or general feature?

Mineral ions are often heterogeneously distributed and present at low concentration in the soil. To optimize the uptake of mineral ions and avoid deleterious effects of uncontrolled mineral uptake, plants need efficient sensing systems that rapidly sense the local external concentrations of nutrients. A plethora of receptors were identified in plant but very few were shown to sense nutrients [52]. Recently, the LRR-RK (leucine-rich repeat receptor kinase) AtSRF3 (Strubbelig receptor kinase 3) was shown to sense external iron levels [53•]. The transcription factors AtNLP7 (NIN-like protein 7) and the bZIP19/bZIP23 (basicregion leucine zipper 19/23) were also shown to sense cellular NO_3^- and Zn^{2+} , respectively [54•,55•]. Although long time regarded as only mediating nutrient transport, more and more nutrient carriers appear to also have a sensing and signaling function. Being the entry point of nutrients in the cell, it appears

rational that nutrient carriers would also sense nutrients as transceptors. To be considered as transceptor, a transporter must be able to bind substrates, triggering a substrate-dependent conformational changes [56]. The first transceptor unequivocally identified in plants was the nitrate transporter AtNRT1.1 (nitrate transporter 1.1) [57,58]. In this case, uncoupling the transport and signaling functions of AtNRT1.1 was the prerequisite to unravel its dual function. Several others transceptors have been proposed since including the influx metal transporter AtIRT1 thought to act as a transceptor, sensing its non-iron metal substrates in the cytoplasm, in turn regulating its own degradation [30]. Similarly, sulfate sensing through AtSULTR1; 2 (Sulfate Transporter 1; 2) has been proposed based on S signaling defects independent of S accumulation in sultr1;2 mutant compare to WT [59,60]. In contrast to AtNRT1.1 and AtIRT1 for which transport and sensing mechanisms can be decoupled, the sensing function of AtBOR1 cannot be decoupled, as residues required for borate transport activity are also necessary for the Bsensing mechanism, regulating its own degradation [61•]. Phosphate level sensing through the binding of inositol pyrophosphate (InsPP) to the SPX domain of several phosphate carriers is another well described mechanism of nutrient sensing and recently illustrated with the VPT1 (vacuolar phosphate transporter 1) phosphate transporter [62-65]. The same sensing mechanism is thought to confer AtPHO1 a P sensing function. Ca^{2+} is a crucial second messenger in signaling pathways known to be involved in responses to Fe, K, and N deficiencies [66-68]. Although not identified yet, Mn^{2+} and K^{+} sensing through putative Ca^{2+} carriers resulting in calcium waves was proposed $[10,69,70\bullet]$. Similarly, the generation of a nitrate-specific Ca²⁺ signature through the interaction between AtNRT1.1/CNGC15 (cyclic nucleotide-gated channel 15) transceptor-channel complex was reported [71•]. As briefly reviewed here, diverse sensing mechanisms exist in plants, allowing them to integrate multiple substrate-dependent regulations, optimize mineral uptake and protect them from excess. Considering the amount of transceptors identified in yeast or mammal cells, we can predict that the plant transceptors identified so far represent only the tip of the iceberg.

Conclusion

Recent works presented in this review highlight the complexity of plant mineral nutrition and the central role played by nutrient carriers. The importance of their cellular/subcellular localization and their polarity for their function appear more striking as new carriers are being characterized. The central role of carriers in nutrition is being reinforced with the identification of sensing functions, which allow fine tuning the plant mineral nutrition. However, despite great advances the field of plant nutrition, the incomplete information on most carriers' localization and the lack of identified carriers in the endodermis particularly, greatly limit our understanding of mineral radial transport. Future work on mineral nutrition will have to tackle this issue.

Declaration of Competing Interest

The authors declare the following financial interests/ personal relationships that may be considered as potential competing interests:Marie Barberon reports financial support was provided by University of Geneva Faculty of Science. Marie Barberon reports a relationship with Swiss National Science Foundation that includes: funding grants.

Data availability

No data was used for the research described in the article.

Acknowledgments

We apologize to authors whose relevant work on nutrient carrier and radial transport of nutrients have not been cited, either inadvertently or because of length constraints. This work was supported by the Sandoz Family Monique De Meuron philanthropic foundation's program for academic promotion and the SNSF (project number PCEGP3_187007) to M.B.

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The authors identified two transcription factors involved in the deposition of polar lignin cap in the exodermis of the tomato root. The paper showed that polar lignin cap has an equivalent barrier function to the endodermal CS. Exodermal and endodermal barriers have yet unique and overlapping roles in mineral selectivity.

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The authors demonstrated that the constitutive activation of the Schengen-pathway induces the deposition of compensatory lignin in the corners of endodermal cells that is chemically distinct from CS lignin. Using ionomic analysis, the authors also show that cell corner lignin can act as an apoplastic barrier to mineral nutrients.

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