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On the Functions of ABC Transporters in Plants

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Abstract

ATP Binding Cassette (ABC) proteins are ubiquitously found in prokaryotes and eukaryotes and generally serve as membrane-intrinsic primary active pumps. In higher plants, ABC proteins constitute a large family, phylogenetically structured into eight clusters, namely the ABCA to ABCI subfamilies [1]. ABC transporters shuttle substrates as diverse as lipids, phytohormones, carboxylates, heavy metals, chlorophyll catabolites and xenobiotic-conjugates across a variety of biological membranes. To date, the largest proportions of characterized members have been localized to the plasma membrane and the tonoplast with dominant implications in cellular secretion and vacuolar sequestration, but they are also found in mitochondrial, plastidal and peroxisomal membranes. Originally identified as tonoplast-intrinsic proteins that shuttle xenobiotic-conjugates from
the cytosol into the vacuole, thus being an integral part of the detoxification machinery, ABC transporters are now recognized to participate in a multitude of physiological processes that allow the plant to adapt to changing environments and cope with biotic and abiotic stresses.

1. Introduction

The plant ABC protein family consists of full-size, half-size and several soluble members that all share a cytosolic nucleotide-binding domain. Functional transport units utilize ATP-hydrolysis to energize the transport of solutes across membranes, independent of concentration gradients and membrane potentials. Full-size members are organized in a modular fashion, consisting of two pore-forming transmembrane domains alternating with two cytosolic nucleotide-binding domains. Half-size members, which contain one transmembrane domain and one nucleotide-binding domain, are thought to form dimers that act as functional units. In most subfamilies, transmembrane domains precede nucleotide-binding domains, a topology which is referred to as forward orientation, while the opposite is considered a reverse orientation [2]. An additional N-terminal transmembrane domain (TMD0) is characteristic to members of the ABCC subfamily. In humans and yeast, the TMD0 of some ABCC proteins was demonstrated to be essential for correct protein targeting, without necessarily having implications in substrate specificity and transport activity [3,4]. The plant soluble ABC proteins cluster in the ABCE, ABCF and ABCI subfamilies. However, due to a primary focus on membrane-intrinsic half- and full-size proteins, they will
not be addressed further in this review. Readers interested in this topic will find information in two comprehensive reviews on plant ABC proteins [2,5].

Genome wide inventories of ABC transporters in Arabidopsis, rice and poplar led to the identification of more than 100 loci encoding for either half-size or full-size transporters in each, making them nearly twice as numerous in plants as reported for sequenced animal species. Half-size (WBC) and full-size (PDR) members of the reverse oriented ABCG subfamily are abundantly found in plants. No full-size ABCG transporters have been identified in animals. It is argued that the expansion and diversification of the ABC protein family in plants may be tightly linked to their autotrophic and sessile lifestyle, requiring a highly plastic development, interaction with the environment and maintenance of basic metabolism under changing conditions.

As a secondary effect of nutrient acquisition from the soil, plants often take up toxic heavy metals, which need to be secreted in order not to interfere with metabolism. One possibility is reflux into the soil or secretion into the foliar apoplast. Full-size ABCG members have been identified as candidates for cadmium and possibly lead export [6,7]. Furthermore, ABC transporters play an important role in the general detoxification mechanism. Extrinsic or intrinsic potentially toxic compounds are first incorporated into conjugates, which are then recognized by tonoplastic ABC transporters and sequestered into the vacuole [8]. Phytohormones are major modulators of plant development and plant responses to biotic and abiotic environmental stimuli. Sites of hormone production differ from sites of hormone action and thus, export from producing cells, directed
distribution within the plant body and specific uptake into receptive cells are crucial for adequate plant function. ABC transporters participate in the translocation of the hormone auxin, a dominant developmental regulator [9], and the hormone abscisic acid (ABA), implicated in abiotic stress responses [10,11]. Plants possess an often species specific array of natural compounds that are produced and deposited in a strictly regulated manner to directly interact with the biotic environment such as deterring herbivores, warding off pathogens and attracting symbionts or pollinators. Their biosynthetic pathways often involve several organelles within a cell and different cell types within an organism. Precursors as well as final products need to be transported across membranes and in several cases ABC transporters are proposed as candidates. Best studied in this respect is the abaxial epidermal deposition of antimicrobial compounds [12,13].

2. Cellular Detoxification

First indications for ABC-mediated transport processes in plants were observed when Martinoia et al. [14] began investigating how xenobiotics are detoxified in plants. They found that potentially toxic compounds, bound to the tripeptide glutathione through their thiol group (glutathione conjugates), are transported into the vacuole independently from the proton motive force generated by two vacuolar proton pumps. Initially, detoxification processes in plants and animals are very similar, involving cytochrome P450 proteins and several transferases, such as glutathione S-transferases, glucuronosyltransferases or
glycosyltransferases [15]. Unlike animals which excrete modified, potentially toxic compounds, plants internalize toxins in large central vacuoles. Two vacuolar glutathione conjugate transporters, AtABCC1/AtMRP1 and AtABCC2/AtMRP2, were identified [16]. Both proteins transport a broad range of glutathione conjugates, glucuronates as well as a chlorophyll catabolite. Later studies have shown that AtABCC1 is an efficient transporter of folates, which are known to be stored in the vacuole and are required for methylation processes [17]. The latter findings suggest that ABCCs are not solely involved in cellular detoxification. Proteomic data obtained for Arabidopsis vacuoles suggest that most ABCCs of Arabidopsis reside in the tonoplast [18], and other ABCCs, additionally to AtABCC1/2, may contribute to the overall glutathione conjugate transport activity. Heavy metals are also stored within the central vacuole for detoxification purposes and data suggest that phytochelatins and phytochelatin heavy metal complexes are transported by ABCC-type transporters [19]. In contrast to S. cerevisiae, where an ABCC-type transporter, YCF1 (yeast cadmium factor 1), catalyzes the transport of glutathion-cadmium complexes [20], and to S. pombe, where Hmt1, a half-size ABC transporter, sequesters phytochelatin [21], the nature of the plant-specific transporter for phytochelatin or heavy metal glutathione complexes is unknown. Some ABCCs can partially rescue the heavy metal sensitivity of the ycf1 yeast mutant [22], but the substrate transported has not been identified.

A member of the AtABCG family, the half-size AtABCG19, confers kanamycin resistance when overexpressed in plants [23]. Since AtABCG19 is highly specific
for kanamycin transport and does not confer resistance to other aminoglycoside antibiotics of clinical importance, the authors propose AtABCG19 as a novel resistance marker for the creation of transgenic plants. Not only would AtABCG19 constitute an endogenous plant-derived marker, it would also limit resistance properties to the antibiotic kanamycin, were it to be transferred horizontally to potentially pathogenic microorganisms.

An alternative way for plants to cope with toxic compounds, soilborne heavy metals in particular, is secretion from the cell, aboveground into the apoplast or cuticle and belowground into the rhizosphere. In Arabidopsis, the plasma membrane-intrinsic full-size AtABCG36/AtPDR8, previously described as pathogen defense related (see also chapter 4.), is involved in the detoxification process [7]. Based on the observation that AtABCG36 expression was promoted by exogenously applied cadmium and lead, the authors tested the response of wild type plants, Atabcg36 knock-out mutants, AtABCG36 silenced mutants and AtABCG36 over-expression mutants to elevated heavy metal concentrations. A clear positive correlation between transcript abundance and resistance to lead and cadmium was established. Furthermore, with respect to the wild type, over-expression lines accumulated less cadmium, and silenced lines more cadmium in root and shoot tissues. Direct involvement of AtABCG36 in the export of cadmium ions or cadmium complexes was demonstrated utilizing isolated mesophyll protoplasts in a $^{109}$Cadmium flux assay. Whereas an over-expressing line proved more efficient in extruding $^{109}$Cadmium than the wildtype, a silenced
line was impaired in its export capacities. The form in which the toxic heavy metal cadmium is transported, whether as free ion or in a chelated form, is unknown.

3. Growth and Development

3.1. Phytate Transport

Inositol hexakisphosphate (InsP₆, phytate) constitutes a major phosphorus store in plants. It accumulates predominantly in seeds as a complex with magnesium, potassium, calcium, iron and/or zinc, representing up to 5% of the seed dry-weight [24,25]. During germination phytate is degraded by phytases, thus providing phosphate, myo-inositol and minerals to developing seedlings. Recent publications revealed that InsP₆ fulfils additional physiological roles. Plants lacking InsP₆ are more susceptible to pathogen attack [26], while in guard cells InsP₆ mobilizes calcium from endomembrane stores and inhibits the inward rectifying K⁺ conductance, thereby influencing stomatal movements [27,28]. InsP₆ can have a negative impact on the environment, since monogastric animals that lack phytases in their digestive tract fail to process the phytates present in seeds. As a consequence, high amounts of undigested phytates are released with the animal waste into nature, thus accentuating the phosphorus pollution from agriculture [29].

During the last few years, low phytate mutants were described in major crop species, i.e. maize, rice and sorghum [30-33]. While in most cases a 45-90% reduction in seed phytate content did not result in detectable phenotypes, some
of the rice mutant lines proved nonviable. In maize, detailed genetic analysis led
to the identification of the ABCC-type transporter ZmMRP4 as the responsible
gene behind InsP$_6$ accumulation in kernels [30]. Phylogenetic studies identified
the tonoplastic AtABCC5/AtMRP5 as the closest Arabidopsis homologue to
ZmMRP4. Atabcc5 loss-of-function mutants display a low InsP$_6$ phenotype in
seed tissue, which is associated with alterations of mineral cation and phosphate
status [34]. Heterologous expression in yeast demonstrated that AtABCC5
encodes a specific high affinity InsP$_6$ transporter. Moreover, complementation of
the Atabcc5 knock-out mutants with an AtABCC5 construct driven by a guard
cell-specific promoter restored the sensitivity of the mutant to ABA–mediated
inhibition of stomatal opening, supporting the hypothesis that InsP$_6$ acts as a
signaling molecule in guard cells. Hence, it is proposed that by transporting InsP$_6$
into the vacuole, AtABCC5 is essential for the regulation of correct stomatal
movement as well as for phytate storage in seeds. One could anticipate that the
elucidation of the InsP$_6$ transport mechanism will contribute to the understanding
of the regulation of various cellular signalling processes. From an applied
perspective it could furthermore address nutritional and environmental questions
regarding the possibility of enhancing the quality of seeds by altering the InsP$_6$
content.

3.2. Import of fatty acids into peroxisomes

Beta-oxidation of fatty acids is a very important catabolic process, required to
generate Acetyl-CoA for entry into the citric acid cycle. In plants it occurs
predominantly within the peroxisomes and thus it requires that fatty acid-CoAs are imported from the cytosol. Arabidopsis loss-of-function mutants of AtABCD1, a full-length peroxisomal ABC transporter, are strongly impaired in germination and display a pleiotropic growth phenotype. These mutants furthermore exhibit an impaired fatty acid metabolism, suggesting that AtABCD1 is the fatty acid-CoA importer in plant peroxisomes [35-37].

3.3. Hormone Transport

Plant development and adaptation to the environment are closely linked to the action of phytohormones. Trytophan derived indole-3-acetic-acid (auxin) is a central phytohormone, implicated in many developmental processes such as shoot elongation, floral bud development, lateral root growth, phototropism and gravitropism [38]. It is mainly produced in the shoot apical meristem, from where it is distributed throughout the plant via cell to cell transport within the xylem parenchyma [38]. Cellular auxin import can either occur simply via diffusion of its protonated form or is catalyzed by members of the AUX1/LAX family of auxin-influx carriers [39]. Polar export was thought to be governed solely by the PIN family of auxin transporters [39]. However, a detailed examination of two plasma membrane-intrinsic ABCB transporters, AtABCB1 and AtABCB19, suggested that ABC transporters also contribute to inter-cellular auxin transport [40]. Atabcb1 and Atabcb19 knock-out plants exhibited slightly retarded growth patterns, while the corresponding double knock-out was strongly impaired in growth, phenotypically reminiscent of auxin deficiency symptoms. Furthermore, auxin
transport in the double knock-out mutant was reduced by more than 70%.

Heterologous expression of AtABCB1 and AtABCB19 in several systems presented direct evidence that both proteins are indeed auxin exporters. Recent studies suggest that the two auxin efflux systems are at least partially interconnected. PIN proteins and ABC transporters interact to modulate the overall auxin transport activity in a complex fashion [41,42]. Furthermore, it was shown that the immunophilin-like protein TWD1 interacts with ABCBs, significantly stimulating auxin transport [43,44]. In contrast to most members of the PIN family, AtABCB1 and AtABCB19 are expressed only in specific cell types. This, in addition to functional overlaps with PIN proteins, may explain why auxin specific ABCB mutant phenotypes are restricted to impairments in cell elongation of shoot and root.

Two recent publications reported that ABC transporters are involved in the transport of the carotenoid-derived stress hormone ABA. Besides being a germination inhibitor present in dormant seeds, ABA is mainly produced in the vasculature of shoots and roots as a response to hydric stress [45,46]. From there it is translocated to foliar tissues, where it induces stomata closure to minimize water loss. Consequently, ABA has to be exported from xylem parenchyma cells, transferred to leaves and imported into guard cells and other cell types to trigger the signaling pathways required for coping with water stress. A half-size transporter in the ABCG family, AtABCG25, is expressed in the vascular parenchyma of root and shoot and was shown to act as an ABA exporter with a high affinity for ABA (apparent Km of 0.2 µM) in heterologous
transport systems [10]. While germination of the corresponding mutant was more sensitive to the application of exogenous ABA, no stomata-specific phenotype could be observed. However, overexpressing AtABCG25 resulted in plants that transpired less water, indicating enhanced ABA export capacities from producing cells. A full-size transporter, AtABCG40, on the other hand, previously proposed to be implicated in heavy metal resistance [6], was found to contribute to the import of ABA across the stomatal plasma membrane [11]. Stomata of Atabcg40 mutant plants close less efficiently when the roots are exposed to ABA and the upregulation of ABA-responsive genes upon ABA treatment is delayed. As a consequence, mutant Atabcg40 plants are more sensitive to drought stress. In heterologous systems, AtABCG40 imports ABA with an apparent Km of 1 µM, which is within the expected physiological range. Still, the exact mechanism by which AtABCG40 achieves the import of its substrate has yet to be investigated. Import mechanisms are well known from bacterial ABC transporters, which catalyze the uptake of nutrients [47]. In contrast, no ABC importers have been described in the animal field. In plants several full-size ABC transporters have been proposed to act as importers (see also chapter 3.2.). Similarly to AtABCG40, AtABCB14 resides in the stomatal plasma membrane, where it is suggested to govern over the import of apoplastic malate, thus influencing stomatal movements in response to changing carbon dioxide concentrations [48]. An interesting case is AtABCB4, where evidence was presented that, depending on the auxin concentration in the cytosol or medium, it can act as importer or
exporter [49]. Further studies concerning structural aspects are pending to unravel the details of ABC-mediated import in plants.

3.4. Cuticle Formation

The plant cuticle is primarily composed of cuticular waxes (aliphatic very long chain fatty acid derivatives), embedded in a cutin matrix (mainly glycerol, C16 and C18 fatty acids) [50]. It covers the epidermis of aerial organs of land plants, forming a protective layer against desiccation and pathogen entry. Proper cuticle deposition is furthermore necessary for organ development, preventing organ fusion and influencing organ morphology. Two half-size ABCG/WBC-proteins, AtABCG11/WBC11 and AtABCG12/WBC12 of Arabidopsis, were demonstrated to play a dominant role in cuticle formation [51,52].

AtABCG12, discovered in a forward screen for wax lacking mutants, is expressed in the epidermal tissues of most plant organs and localizes to the plasma membrane, where it is proposed to play a direct role in the export of a multitude of wax precursors [51]. Stem epidermal cells of Atabcg12 knockout plants feature laminar cytoplasmic inclusions of lipidic nature and the stem cuticle is depleted in a variety of wax components such as long chain alkanes, ketones and alcohols, giving the stem a glossy bright green appearance. In contrast, the total amount of epidermal wax, intracellular and cuticular, does not differ between WT and mutant, suggesting that the cytosolic inclusions comprise an accumulation of wax components that are lacking in the cuticle due to transport defects.
AtABCG11 transcript is predominantly found in the epidermis of aerial organs. The protein localizes to the plasma membrane, with a marked polar distribution on the distal epidermal side in developing embryos [53]. In congruence with AtABCG12 function, it contributes to the secretion of cuticular waxes and loss-of-function results in an aberrant cuticle structure [52]. In contrast to Atabcg12, Atabcg11 also displays a reduced cutin load, suggesting cutin precursor fatty acids as additional substrates. The cuticle is one of the main barriers against non-stomatal water loss. Thus, it was intriguing to find that the water stress related hormone ABA induces upregulation of AtABCG11 [54], which is speculated to enhance fortification of aerial organs against desiccation. Consistent with this finding, Atabcg11 mutants are prone to wilting, but more conspicuously, they display a pleiotropic growth phenotype, with a marked reduction in growth, fusion of rosette leaves, altered reproductive organs and sterility. Double mutants of AtABCG12 and AtABCG11 do not exhibit an additive phenotype [55]. Consequently it was suggested that they form heterodimers, with a strong affinity for cuticular waxes. The additional cutin phenotypes of Atabc11 mutants suggest that AtABCG11 can also form homodimers or heterodimers with half-size ABCG members other than AtABCG12 to create a complex with a high affinity for cutin precursor fatty acids.

4. Pathogen Defense
Anti-microbial plant secondary metabolites such as terpenoid derivates and cyanogenic glycosides form an important first line of defense against host and non-host pathogens [56]. They inhibit the proliferation of fungal and bacterial microbes on aerial plant surfaces, within the rhizosphere and in the apoplast around local infection sites. There is increasing evidence that the aboveground and belowground secretion of such compounds is in part mediated by full-size ABC transporters of the ABCG/PDR subfamily. Transcript profiling of ABCG members in rice [57] revealed that nearly half of them positively respond to jasmonic acid (JA) and/or salicylic acid (SA), two phytohormones implicated in biotic stress responses. This suggests roles in pathogen defense, which is supported by the finding that three full-length ABCGs are induced in rice leaves that are infected with the biotrophic fungus *Magnaporthe grisea*. Belowground, loss-of-function of AtABCG30/AtPDR2 results in a drastic change of soil microflora in the rhizosphere [58], which the authors attribute to a change in root-exudate composition. Additionally, the overall profile of root exudates is altered in several ABC transporter mutants [59].

Particularly within the rhizosphere, plant-derived secondary compounds serve as powerful attractants for beneficial microbes such as mycorrhizal fungi and rhizobacteria. Specific inhibitor studies suggest that ABCG subfamily members are responsible for the secretion of genistein and daidzein, both iso-flavonoids that act as plant-derived signaling molecules in the legume-rhizobia symbiosis, into the rhizosphere [60,61].
Functional characterization of NpPDR1, a full-size ABCG protein of *Nicotiana plumbaginifolia*, was the first report of a plant ABC transporter being implicated in pathogen defense and the first description of active terpenoid transport in plants [62]. NpPDR1 resides in the plasma membrane and is induced by the anti-fungal diterpenes sclareol and sclareolide. In isolated microsomes NpPDR1 contributes to the transport of radiolabeled compounds closely related to sclareol, supporting the hypothesis that sclareol is a natural substrate. *NpPDR1* transcript is most abundant in the leaf epidermis, including leaf trichomes, but is also present in root tissues and petals [13]. Apart from its proposed substrate sclareol, both JA and SA promote *NpPDR1* expression, indicating association with defense-related signaling pathways. Concomitantly, a strong response to *Botritis cinerea* and *Pseudomonas syringae*, both necrotrophic non-host pathogens, is observed. Downregulation of NpPDR1 lead to spontaneous and commonly lethal infections with *B. cinerea* and rendered the plant highly susceptible to exogenously applied sclareol. All these findings indicate a participation of NpPDR1 in basal plant defense. It is hypothesized that antimicrobial compounds such as sclareol are deposited via NpPDR1 on the leaf surface and possibly exuded into the rhizosphere, contributing to a constitutive chemical defense barrier. Upon perception of various pathogens and transduction via JA and SA dependent pathways this mode of defense is intensified locally around areas of infection, so that NpPDR1-mediated modes of action are both constitutive and induced.

*AtABCG36/AtPDR8/PEN3* was first recognized as a crucial factor in pre-invasive nonhost resistance in an extensive forward genetic screen of Arabidopsis
mutants for an increased susceptibility to the barley powdery mildew pathogen
[12]. The AtABCG36 loss-of-function mutants were compromised in their capacity
to prevent entry of two nonhost biotrophs and one nonhost necrotroph. However,
they proved hyperresistant against the compatible Arabidopsis powdery mildew
pathogen, which the authors attribute to a hyperactivation of SA-dependent
pathways observed in the mutant. GFP-fusion construct under the control of the
native promoter complemented the phenotype and the corresponding fusion
protein was targeted to the plasma membrane, with increased fluorescence
intensities at infection sites. The authors hypothesize that AtABCG36 transports
defense related compounds across the plasma membrane in a concentrated
manner at local infection sites. Lack of AtABCG36 function would lead to an
accumulation of these compounds within the cell, which may activate SA
dependent pathways that prime defense against compatible pathogens.

Recently a full-size ABCG was identified as the responsible gene behind a robust
and durable pathogen resistance against leaf rust, stripe rust and powdery
mildew in wheat carrying functional LR34 (Leaf Rust 34) alleles [63]. Unlike many
other ABCGs, its expression seems to be modulated by developmental cues
rather than stress factors. LR34 is predominantly found in adult foliar tissues,
particularly the flag leaf. Transcript abundance is highest in the leaf tip and wheat
varieties with functional LR34 alleles can be phenotypically selected via a leaf tip
necrosis developing in adult flag leaves. Despite its resistance conferring
properties, LR34 is not responsive to pathogen inoculation, suggesting rather
constitutive than induced functions. In contrast to NpPDR1 and AtABCG36
function, which seem restricted to nonhost resistance, LR34 is implicated in the
defense against several compatible pathogens of fungal origin. LR34 is the only
ABCG protein characterized to date, that impedes the invasion and spread of
compatible pathogens. Research with focus on the nature of its substrates is
ongoing.

Considering the participation of ABCG transporters in secondary metabolite-
based pathogen response, it is reasonable to assume that they also play a role in
herbivory defense, e.g. via the deposition of insect-deterring compounds on leaf
surfaces. Certain compounds of terpenoid origin are known to act as herbivore
deterrents and JA, a potent inducer of many full-size ABCGs, is also a major
mediator of herbivory responses.

5. Conclusion

The functional study of plant ABC transporters is a rapidly expanding field. It is
becoming increasingly apparent that ABC dependent transport processes not
only serve to protect the plant from endogenous and exogenous toxic
compounds, but that they are indispensable for proper development, adequate
interaction with the environment and basic metabolic processes.

There seems to be no clear functional separation among the different subfamilies,
but from our current knowledge it is possible to define subfamily specific
preferences. Members of the ABCB subfamily have been mainly implicated in
organic acid transport across the plasma membrane and it is probable that other
members serve similar functions, e.g. in the excretion of carboxylates for either
cytosolic pH homeostasis or rhizosphere acidification. Secondary compounds of terpenoid origin and highly lipophilic compounds are common substrates for members of the ABCG clade. The question remains whether ABCG proteins might also display specificity for other secondary compound classes such as alkaloids and flavonoids. Biotechnological approaches to produce natural compounds of medicinal value in heterologous or modified tissue culture systems are currently pursued with emphasis to supply the pharmaceutical market. Understanding and designing highly productive systems must necessarily include efficient transport mechanisms to relocate precursors within the manufacturing units and to excrete final products into the medium. The ability of several subfamily members to efficiently sequester xenobiotic compounds and heavy metals is also of importance to the biotechnological market. Attempts to detoxify contaminated soils via phytoremediation, utilizing genetically modified plants, are underway. Altered expression of certain ABC transporters appears to be part of a feasible approach, for example, to prevent reflux of extracted contaminants into the soil and enhance vacuolar accumulation in foliar tissues. The novel findings that ABCG members are participating in ABA transport are intriguing and tempt us to speculate that the translocation of hormones other than ABA and auxin might also rely on ABC-dependent mechanisms. Possible candidates falling into the predicted substrate range of ABCGs are the recently discovered branching hormone strigolactone [64,65], an apocarotenoid structurally related to ABA, and the brassinosteroids, highly lipophilic terpenoid derivates.
ABC proteins play an important role in plant growth and development. The function of most of plant ABC proteins still awaits elucidation. Functional redundancies render classical mutagenesis-based forward- or reverse-genetic approaches futile. Producing multiple loss-of-function mutants of closely related ABC transporters, and/or finding their interacting partners might reveal additional functions that will direct the studies on plant ABC transporters.

6. Summary

- Higher plants contain more than one hundred ABC proteins that are organized in eight clusters, namely ABCA to ABCI subfamilies, and predominantly localize to the plasma membrane and tonoplast.

- Most ABCCs/MRPs localize to the tonoplast where several of them are thought to catalyze the vacuolar sequestration of xenobiotic-conjugates.

- AtABCG36 plays a role in heavy metal tolerance, as well as in pathogen defense, but the nature of the respective substrates has yet to be determined.

- AtABCC5 is a tonoplastic phytate transporter with implications in phytate storage in seeds and regulation of stomatal movement.
• Several ABCBs/PGPs are participating in a directional cell to cell transport of auxin via polar export and interaction with other auxin transporters.

• Two ABCGs contribute to the inter-cellular transport of the apocarotenoid stress hormone ABA.

• Two half-size ABCGs/WBCs contribute to cuticle formation via the epidermal excretion of cuticular wax components.

• Several full-size ABCGs/PDRs have been implicated in pathogen defense supposedly via excretion of anti-microbial secondary metabolites.

• AtABCB14 localizes to the plasma membrane of guard cells and catalyzes the import of malate, thus influencing stomatal movement.

7. References


gene 5 result in reduction of phytic acid in rice seeds. Theor Appl Genet 119, 75-83.


8. Figure legends

Figure 1. Arabidopsis ABC transporters in different organs with their substrate and/or function.

Figure 2. Tissue level localization of Arabidopsis ABC transporters with their substrates

(a) Mesophyll and epidermal cells. AtABCC1 and AtABCC2 reside on the tonoplast and mediate the transport of xenobiotic compounds and endogenous metabolites into the vacuole. AtABCG11/12 are polarly localized on the plasma membrane and export lipids used for cuticle formation. AtABCG36 is a resistance
factor for pathogens. (b) Guard cell. AtABCG40 acts as an ABA importer from the apoplast into the cytosol and mediates ABA induced stomatal closure. The tonoplast localized AtABCC5 transports InsP₆ (IP₆) into the vacuole thereby lowering the active pool of InsP₆ in the cytosol. AtABCB14 is a plasma-membrane malate importer that acts during stomatal movements. The major outward current of malate during stomatal closure is indicated with a gapped blue arrow. (c) Transection through a root. AtABCG25 is polarly localized on the plasma membrane of parenchyma cells where it mediates ABA export from parenchyma cells into the xylem stream. AtABCG36 has been shown to export toxic cadmium ions that have unspecifically entered epidermal cells. AtABCG30 is an exporter for root exudates and residues on the plasma membrane of root epidermal cells.
Figure 1

**Seeds**
- **AtABCC5**
  - InsP₆ loading into seeds
- **AtABCG11/12**
  - Organ fusion prevention

**Shoot**
- **AtABCB1/19**
  - Auxin transport
- **AtABCG11/12**
  - Cuticle formation
- **AtARCG36**
  - Pathogen defense
- **AtABCC1/2**
  - Detoxification

**Leaf**
- **AtABCG40**
  - ABA import
- **AtABCB14**
  - Stomatal regulation
- **AtABCC5**
  - InsP₆ import
- **AtABCG11/12**
  - Cuticle formation

**Roots**
- **AtABCG25**
  - ABA export
- **AtABCG36**
  - Heavy metal transport
- **AtABCG30**
  - Excretion of exudates
10. Key words
Arabidopsis thaliana

ABCB/PGP subfamily
ABCC/MRP subfamily
Half-size ABCG/WBC subfamily
Full-size ABCG/PDR subfamily
Export and Import
Cellular detoxification
Phytate transport
Hormone transport
Stomatal movements,
Cuticle formation
Pathogen defense
Transport of natural compounds