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2021 update on ATP-binding cassette (ABC) transporters: how they meet the needs of plants

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Introduction

ATP-binding cassette (ABC) proteins bind ATP, hydrolyze ATP, and use the energy released from the reaction to drive transport or regulate cellular functions. The plant ABC protein family is classified into eight subfamilies: A–G and I (Verrier et al., 2008). Most ABC proteins form membrane transporters that consist of two nucleotide-binding domains (NBDs) and two transmembrane domains (TMDs). Full-size ABC proteins alone form functional transporters, but many half-size ABC proteins or some bacterial-type intrinsic members form multisubunit complexes to perform their functions. While NBDs are highly conserved among ABC proteins, TMDs vary, allowing the transport of many different substrates. For the detailed structural and phylogenetic characteristics of plant ABC proteins, refer to previous reviews (Verrier et al., 2008; Kang et al., 2011).

In plants, which generally contain more ABC proteins than most other living organisms, these proteins facilitate the transport of diverse substrates and regulate multiple physiological processes (Hwang et al., 2016; Tables 1, 2). The substrates of plant ABC proteins include hormones, pigments, toxic chemicals, secondary metabolites important for defense, lipidic molecules, and reactive oxygen species (ROS)-related compounds (Jasiński et al., 2001; Footitt et al.,

ADVANCES

- New research reveals plant ABC proteins have critical functions throughout the plant life cycle. Some members of the ABCF and ABCI subfamilies play roles unrelated to transport, expanding the range of functions of plant ABC proteins.
- Recent reports provide hints as to how plant ABC proteins perform such diverse functions. Various factors contribute to the diversity of ABC transporter functions, including their great numbers, the high percentage of genes encoding half-size transporters that can dimerize with different partners, post-translational modifications, and alternative splicing of transcripts. Such mechanisms might have evolved to help plants adapt to the ever-changing environment and internal needs.
- Recent evolutionary studies of plant ABC proteins yield interesting ideas for further study.

2002; Goodman et al., 2004; Geisler et al., 2005; Song et al., 2010; Do et al., 2019). In some cases, a single ABC protein is thought to transport many chemically unrelated substrates. However, some of these candidate substrates might be indirectly altered in concentration in a compartment, rather than directly transported by the ABC protein. It is difficult to test the substrate specificity rigorously using current technology, especially for ABC proteins, which have a tremendous range of substrates. Tables 1, 2 summarize the physiological roles of plant ABC transporters, the candidate substrates suggested based on the physiological roles, and the substrates that have been characterized using direct transport assays. Some excellent reviews and recent reports are available on ABC proteins involved in hormone transport (Geisler et al., 2017; Kang et al., 2017; Park et al., 2017; Ofori et al., 2018; Aryal et al., 2019; Borghi et al., 2019; Feng et al., 2019; Krattinger et al., 2019; Liu et al., 2019; Pawela et al., 2019; Zhao et al., 2019; Wang et al., 2020). This topic will not be covered in this review due to space limitations.

Here, we focus on developments that have occurred in the field of ABC proteins since our previous review (Hwang et al., 2016), including newly identified functions and regulatory mechanisms and insight into how these proteins contribute to the development and physiology of terrestrial plants. These findings support the idea that ABC proteins transport a wide range of substrates essential for plant survival under dry conditions. Furthermore, we discuss interesting future research directions (see "Outstanding questions") and potential applications (Box 1) of ABC proteins in plants.

Newly characterized ABC proteins

Development

ABCG functions in development by transporting surface coating materials

Proper surface coating by lipid transporters including Arabidopsis (*Arabidopsis thaliana*) ABCG11, ABCG12, and ABCG13 is essential from the beginning of plant development to reproduction (Pighin et al., 2004; Panikashvili et al., 2010). Numerous homologs and orthologs of these genes are involved in various aspects of plant development (also reviewed in Do et al., 2018). STIGMA EXSERTION1 (SGE1) and MtABCG13, the Medicago (*Medicago truncatula*) orthologs of AtABCG11 and AtABCG13, respectively, play roles in determining SGE (Zhu et al., 2020), an important agricultural trait for the utilization of heterosis in crop breeding. The use of self-pollinating legume plants such as soybean (*Glycine max*) and Medicago for heterosis is limited due to their complex fused floral architecture, in which the pistil is covered by petals. However, in the *mtsge1* mutant, the stigma is exposed to the outside of the flower because the petals fail to expand and cover the stigma due to a lack of cutin and wax. MtSGE1 can dimerize with MtABCG13, and *mtabcg13* exhibits a similar phenotype to *mtsge1*, suggesting that the MtSGE1/MtABCG13 dimer transports cutin/wax components for petal surface coating (Zhu et al., 2020).

OsABCG9 in rice (*Oryza sativa*) mainly functions as a wax transporter, in contrast to its Arabidopsis ortholog AtABCG11, a cutin/wax transporter (Panikashvili et al., 2010; Nguyen et al., 2018). OsABCG9 is primarily expressed in shoots at the vegetative stage. In *osabcg9* plants, the cuticular wax load is reduced by half, but cutin levels are not; this mutant exhibits growth retardation and enhanced susceptibility to drought stress (Nguyen et al., 2018). OsABCG15, OsABCG26, and OsABCG3 function in pollen development (Zhao et al., 2015; Chang et al., 2018). OsABCG3 is specifically expressed in anthers at pollen development Stages 9–10, and its loss of function causes male sterility, similar to that observed for loss of OsABCG15 and OsABCG26 function (Zhao et al., 2015; Chang et al., 2018). However, OsABCG3 functions specifically in pollen wall formation (nexine II and intine layers), while OsABCG15 and OsABCG26 function broadly in pollen wall, pollen coat, and anther cuticle formation (Zhao et al., 2015; Chang et al., 2018). In Arabidopsis, ABCG5 functions as a wax transporter, which is important for early seedling establishment (Lee et al., 2020). When grown under waterlogged conditions, *atabcg5* plants had water-soaked cotyledons and experienced hypoxic stress due to reduced cuticular wax content, leading to water permeation into the cotyledons. The *atabcg5* seedlings failed to develop true leaves under these conditions. Both recent and previous studies of ABCG transporters of surface coating materials (reviewed in Do et al., 2018) demonstrated that the hydrophobic barrier on the plant surface is essential for proper plant development by providing the lubrication needed for organ separation and protecting the plant from both excess water and dry air by limiting water movement through its surface.

ABCG functions in development by transporting redox-related compounds

The regulation of cell redox status is critical for plant survival in oxygen-rich terrestrial environments. The Arabidopsis ABC transporter of the mitochondria 3 (AtATM3)/AtABCB25 functions in Fe–S cluster formation (Kushnir et al., 2001) by exporting glutathione polysulfide from the mitochondria for cytosolic Fe–S cluster assembly (Schaedler et al., 2014). The rice ortholog OsATM3 was recently shown to be essential for cytosolic Fe–S cluster assembly and, thus, meristem maintenance (Zuo et al., 2017). The *osatm3* mutation results in lethality at the four-leaf stage due to a defect in Fe–S cluster biosynthesis and the hyperaccumulation of superoxide anion (Zuo et al., 2017).

Tip-growing cells such as pollen tubes and root hairs require tip-focused ROS for continuous growth. An Arabidopsis half-size ABCG with a unique topology is critical in establishing proper ROS levels at the tips of these structures (Do et al., 2019). This transporter, AtABCG28, is expressed specifically in mature pollen and growing pollen tubes and localizes to the membranes of secretory vesicles. AtABCG28 is involved in sequestering polyamines (source of ROS) into the vesicles that move and fuse to the growing

Table 1 Summary of the physiological functions of plant ABC proteins identified to date

Physiological function	ABC proteins involved	References[a]
Secretion of surface coating materials		
Cutin and wax precursors	AtABCG5, AtABCG11, AtABCG12, AtABCG13, AtABCG32, OsABCG9, OsABCG15, OsABCG26, OsABCG31, MtSGE1, MtABCG13, PpABCG7, HvABCG31	Pighin et al. (2004); Bird et al. (2007); Bessire et al. (2011); Chen et al. (2011); Panikashvili et al. (2011); Buda et al. (2013); Qin et al. (2013); Zhao et al. (2015); Garroum et al. (2016); Nguyen et al. (2018); Lee et al. (2020); Zhu et al. (2020)
Suberin precursors	AtABCG1, AtABCG2, AtABCG6, AtABCG11, AtABCG20, OsABCG5, StABCG1	Panikashvili et al. (2010); Landgraf et al. (2014); Shiono et al. (2014); Yadav et al. (2014); Fedi et al. (2017); Shanmugarajah et al. (2019)
Lignin precursors	AtABCG29	Alejandro et al. (2012)
Pollen wall and coat materials	AtABCG1, AtABCG9, AtABCG16, AtABCG26, AtABCG31, OsABCG3, OsABCG15, OsABCG26	Quilichini et al. (2010); Qin et al. (2013); Choi et al. (2014); Yadav et al. (2014); Zhao et al. (2015); Chang et al. (2018)
Hormone transport and signaling		
Cytokinins	AtABCG14, OsABCG18, VviABCG14, VviABCG7, MdABCG28, AtABCI19, AtABCI20, AtABCI21	Ko et al. (2014); Zhang et al. (2014); Feng et al. (2019); Zhao et al. (2019); Kim et al. (2020); Wang et al. (2020)
ABA	AtABCG25, AtABCG40, AtABCG30, AtABCG31, MtABCG20, TaLr34, AaABCG40	Kang et al. (2010); Kuromori et al. (2010); Kang et al. (2015); Krattinger et al. (2019); Pawela et al. (2019)
Auxins and precursors	AtABCB1, AtABCB4, AtABCB14, AtABCB15, AtABCB19, AtABCB21, AtABCG1, AtABCG16, AtABCG36, AtABCG37, LjABCB1, OsABCB14, ZmABCB1, SlABCB4	Geisler et al. (2005); Lin and Wang (2005); Santelia et al. (2005); Terasaka et al. (2005); Knöller et al. (2010); Ruzicka et al. (2010); Kaneda et al. (2011); Kamimoto et al. (2012); Takanashi et al. (2012); Xu et al. (2014); Ofori et al. (2018); Aryal et al. (2019); Fu et al. (2020); Liu et al. (2020a, 2020b)
JA and JA-Ile	AtABCG16	Li et al. (2017)
SL	PhPDR1, PaPDR1, MtABCG59	Kretzschmar et al. (2012); Sasse et al. (2015); Banasiak et al. (2020)
Regulation of cellular redox state		
Transport of Fe–S cluster precursor	AtABCB25 (ATM3), OsATM3	Schaedler et al. (2014); Zuo et al. (2017)
Sequestering polyamines	AtABCG28	Do et al. (2019)
Intracellular metabolite transport		
Phytic acid	AtABCC5, ZmMRP4, OsMRP5, TaABCC13, BnMRP5	Shi et al. (2007); Nagy et al. (2009); Xu et al. (2009); Bhati et al. (2016); Sashidhar et al. (2020)
Lipid transfer	AtABCD1, AtABCA9, AtABCI14 (TGD1), AtABCI15 (TGD2), AtABCI13 (TGD3)	Xu et al. (2003); Awai et al. (2006); Lu et al. (2007); Nyathi et al. (2010); Kim et al. (2013)
Defense against infection or herbivory		
Secretion of defense molecules	AtABCG34, AtABCG36, AtABCG40, NtPDR1, SpTUR2, CrTPT2, MtABCG10, TaLr34, NtABCG5, VmABCG1	van den Brûle et al. (2002); Bienert et al. (2012); Crouzet et al. (2013); Yu and De Luca (2013); Lu et al. (2015); Biala et al. (2017); Demessie et al. (2017); Khare et al. (2017); He et al. (2019); Rajagopalan et al. (2020)
Translation regulation	AtABCF4 (GCN4), AtABCF3 (GCN20), LrABCF1	Sun et al. (2016); Kaundal et al. (2017); Han et al. (2018)
Accumulation of defense molecules	AtABCC2, VvABCC1, CsABCC4a, CsABCC2, ZmMRP3, CjABCB1, CjABCB2	Shitan et al. (2003); Goodman et al. (2004); Francisco et al. (2013); Shitan et al. (2013); Behrens et al. (2019); Demurtas et al. (2019)
Metal homeostasis		
Chloroplast	AtABCI11 (NAP14), AtABCI10, AtABCI12, OsABCI7	Voith von Voithenberg et al. (2019); He et al. (2020)
Mitochondria	AtATM1, AtATM3	Chen et al. (2007); Teschner et al. (2010)
Regulation of stomatal aperture via malate transport	AtABCB14	Lee et al. (2008)
Nutrient acquisition from the soil under iron deficiency	AtABCG37,NtPDR3	Fourcroy et al. (2014); Ziegler et al. (2017); Lefèvre et al. (2018)
Attracting pollinators by releasing VOCs	PhABCG1	Adebesin et al. (2017)
Self-incompatibility	MdABCF, PiABCF	Meng et al. (2014)
Regulation of the root microbiome via root exudate secretion	AtABCG30, AtABCG37	Badri et al. (2009); Ziegler et al. (2017)
Detoxification by sequestering heavy metals and toxic organics	AtABCC1, AtABCC2, AtABCC3, AtABCG36, AtABCG40, AtABCB27 (ALS1), AtABCI16 (ALS3), AtSTAR1, OsALS1, OsABCG36, OsSTAR1, OsSTAR2, PtoABCG36, PtABCC1, FeALS1.1, FeALS1.2, FeSTAR1, FeSTAR2, HvABCB25	Larsen et al. (2005); Lee et al. (2005); Kim et al. (2007); Larsen et al. (2007); Huang et al. (2009); Huang et al. (2010); Song et al. (2010); Huang et al. (2012); Park et al. (2012); Brunetti et al. (2015); Che et al. (2018); Sun et al. (2018); Fu et al. (2019); Wang et al. (2019a, 2019b); Liu et al. (2020a, 2020b)

[a]Due to space limitations, representative publications are cited for individual ABC transporter proteins and their associated functions.

Table 2 Summary of plant ABC transporter proteins of which substrates have been characterized by transport assays using single-cell systems or purified protein of interest

ABC protein	Substrates	Transport assays[a]	References
ABCA[b]			
ABCB			
AtABCB1	IAA and NAA	^{3}H-IAA and ^{3}H-NAA transport of *atabcb1* mesophyll protoplasts; ^{3}H-IAA and ^{3}H-NAA transport of *Saccharomyces cerevisiae* JK93da expressing AtABCB1; ^{3}H-IAA transport of *Schizosaccharomyces pombe* expressing AtABCB1; ^{3}H-IAA and ^{3}H-NAA transport of HeLa cells expressing AtABCB1	Geisler et al. (2005); Yang and Murphy (2009); Kamimoto et al. (2012)
AtABCB4	IAA and NAA	^{3}H-IAA and ^{3}H-NAA transport of BY-2 cell lines expressing AtABCB4; ^{3}H-IAA transport of *S. cerevisiae* JK93da expressing AtABCB4; ^{3}H-IAA transport in *S. pombe* expressing AtABCB4; ^{3}H-IAA transport of HeLa cells expressing AtABCB4	Terasaka et al. (2005); Kamimoto et al. (2012); Kubeš et al. (2012)
AtABCB14	Malate	^{14}C-malate transport of *Escherichia coli* strain *dct* expressing AtABCB14; ^{14}C-malate transport of HeLa cells expressing AtABCB14	Lee et al. (2008)
AtABCB19	IAA and NAA	^{3}H-IAA accumulation of *S. pombe* expressing AtABCB19; ^{3}H-IAA transport of HeLa cells expressing AtABCB19	Yang and Murphy (2009); Kubeš et al. (2012)
AtABCB21	IAA	^{3}H-IAA transport of *atabcb21* knock-down mesophyll protoplasts cells; ^{3}H-IAA transport of *S. cerevisiae* JK93da expressing AtABCB21	Kamimoto et al. (2012)
AtABCB25 (AtATM3)	Glutathione polysulfide	ATP hydrolysis of AtABCB25 expressed and purified in *Lactoccocus lactis*; ^{35}S-GSSG transport of vesicles derived from *L. lactis* expressing AtABCB25	Schaedler et al. (2014)
LjABCB1	IAA	Auxin transport using heterologous cells expressing LjABCB1	Takanashi et al. (2012)
OsABCB14	IAA	IAA transport of yeast strain expressing OsABCB14; IAA transport of rice protoplasts derived from *osabcb14*	Xu et al. (2014)
SlABCB4	IAA	IAA transport of *N. benthamiana* protoplasts expressing SlABCB4	Ofori et al. (2018)
ABCC			
AtABCC1	GS conjugates and chlorophyll catabolites	Uptake of ^{14}C–Bn-NCC-1, ^{3}H–DNP-GS, ^{3}H-GSSG, and ^{14}C–Metolachlor-GS by vacuolar membrane purified from *S. cerevisiae* DTY168 expressing AtMRP1	Lu et al. (1998)
	As(III)-PC2	As-PC transport of vesicles derived from *S. cerevisiae* expressing AtABCC1	Song et al. (2010)
	Folate monoglutamates and antifolates	Transport of ^{3}H-folate monoglutamates and antifolates of vacuolar vesicles derived from *atabcc1* and yeast strain DTY168 expressing AtABCC1	Raichaudhuri et al. (2009)
	ABA-GE	Transport of ^{14}C- or ^{3}H-ABA-GE into vesicles derived from yeast strain YMM36 expressing AtABCC1	Burla et al. (2013)
AtABCC2	GS conjugates and chlorophyll catabolites	Uptake of ^{14}C–Bn-NCC-1, ^{3}H–DNP-GS, ^{3}H-GSSG, and ^{14}C–Metolachlor-GS by vacuolar membrane purified from *S. cerevisiae* DTY168 expressing AtMRP2	Lu et al. (1998)
	Anthocyanins, Flavone, Flavonol glucosides	Anthocyanins and flavonoids transport of vesicles derived from yeast strain DTY168 expressing AtABCC2	Behrens et al. (2019)
	As(III)-PC2	As-PC transport of vesicles derived from *S. cerevisiae* expressing AtABCC2	Song et al. (2010)
	ABA-GE	Transport of ^{14}C- or ^{3}H-ABA-GE into vesicles derived from yeast strain YMM36 expressing AtABCC1	Burla et al. (2013)
AtABCC3	GSH conjugate and chlorophyll catabolite	Uptake of ^{14}C-DNB-GS and ^{14}C-Bn-NCC by vesicles derived from yeast strains expressing AtABCC3	Tommasini et al. (1998)
AtABCC4	Antifolates	^{3}H-methotrexate transport of vesicles derived from yeast strain Δycf1Δbpt1	Klein et al. (2004)
	Inositol hexakisphosphate	^{33}P-inositol hexakisphosphate uptake into microsomes isolated from yeast ycf1 expressing AtMRP5	Nagy et al. (2009)
AtABCC5	Glutathione conjugate and glucuronide conjugate	Uptake of ^{14}C-glutathione conjugate and ^{3}H-glucuronide conjugate into microsomes from yeast DTY168 expressing AtMRP5	Gaedeke et al. (2001)
OsABCC7	As(III)-phytochelatin and As(III)-glutathione	Efflux assay using *Xenopus laevis* oocytes expressing OsABCC7	Tang et al. (2019)
VvABCC1	Glucosylated anthocyanidins	Malvidin 3-O-glucoside transport of vesicles derived from yeast strain *ybt1* expressing VvABCC1	Francisco et al. (2013)

(continued)

Table 2 Continued

ABC protein	Substrates	Transport assays[a]	References
CsABCC4a and CsABCC2	Crocins	Crocins uptake using microsomes from *S. cerevisiae* expressing CsABCC4a and CsABCC2	Demurtas et al. (2019)
ABCD			
AtABCD1/CTS	Fatty acyl-CoAs with various carbon chain	Fatty acyl-CoAs induced ATPase activity of peroxisomes derived from *S. cerevisiae* expressing AtABCD1	Nyathi et al. (2010)
ABCE[b]			
ABCF[b]			
ABCG			
AtABCG1	Long-chain fatty acids and fatty alcohol	ATPase assay with heterologously expressed and purified AtABCG1 in *Pichia pastoris*	Shanmugarajah et al. (2019)
AtABCG16	JA and JA-Ile	^{3}H-JA transport of yeast strain expressing AtABCG16; transport of ^{3}H-JA and ^{3}H-JA-Ile by the nuclei isolated from *atabcg16* plant	Li et al. (2017)
AtABCG25	ABA	ABA transport assay in membrane vesicles derived from AtABCG25-expressing Sf9 insect cells	Kuromori et al. (2010)
AtABCG29	*p*-coumaryl alcohol	*p*-coumaryl alcohol uptake using microsomes from *S. cerevisiae* expressing AtABCG29	Alejandro et al. (2012)
AtABCG30	ABA	^{3}H-ABA transport of yeast strains expressing AtABCG30	Kang et al. (2015)
AtABCG31	ABA	^{3}H-ABA transport of yeast strains expressing AtABCG31	Kang et al. (2015)
AtABCG37	IBA, 2,4-D	^{3}H-IBA export from *abcg37* leaf mesophyll protoplasts ; ^{3}H-IBA transport in yeast strains expressing AtABCG37; export of ^{3}H-2,4-D and ^{3}H-IBA in HeLa cells expressing AtABCG37	Ruzicka et al. (2010)
AtABCG40	ABA	^{3}H-ABA uptake in yeast strain YMM12 and BY-2 cell lines expressing AtABCG40	Kang et al. (2010)
AaABCG40	ABA	ABA transport of yeast strain expressing AaABCG40	Fu et al. (2020)
MtABCG20	ABA	ABA efflux from BY2 cell lines overexpressing MtABCG20; ATP-dependent ^{3}H-ABA transport in membrane vesicles derived from BY2 cells overexpressing MtABCG20	Pawela et al. (2019)
OsABCG18	CK	Export assay with heterologous expression of OsABCG18 in *N. benthamiana* protoplasts	Zhao et al. (2019)
OsABCG36	Cd or Cd conjugate	Efflux activity with heterologous expression in yeast cells	Fu et al. (2019)
TaABCG36 (Lr34)	ABA	^{3}H-ABA transport of yeast strains W303 and YMM12 expressing Lr34	Krattinger et al. (2019)
PhABCG1	Methylbenzoate and benzyl alcohol	^{14}C-methylbenzoate and benzyl alcohol transport of BY2 cells expressing PhABCG1	Adebesin et al. (2017)
NtPDR1	Diterpenes and sesquiterpenes	Diterpenes (sclareol and cembrene) and sesquiterpenes (capsidiol) enhanced ATPase activity of purified NtPDR1-reconstitued liposomes	Pierman et al. (2017)
ABCI[b]			

[a]Brief methods of transport assays from literature cited are listed in no particular order.
[b]None of these subfamily members have been characterized for substrate transport via transport assay.

tip. Therefore, AtABCG28 confines the site of ROS production to the growing tip, thereby contributing to tip growth and protecting the cytosol from ROS damage (Figure 1). Various other ABCG proteins with similar domain structures to AtABCG28 might also contribute to the polar distribution of intracellular ROS by sequestering ROS sources to secretory vesicles.

ABCCs function in development via phytic acid transport

Several AtABCC5 orthologs have been identified in crop plants as potential vacuolar transporters for phytic acid, which enable phytic acid to accumulate in the vacuole and mediate its removal from the cytosol (Bhati et al., 2016; CominelLi et al., 2018, 2020; Sashidhar et al., 2020). Phytic acid functions as a major storage of phosphorus, but it is also an anti-nutritional factor that reduces mineral absorption from the diet (Cominelli et al., 2020). AtABCC5

orthologs have been an important target gene for the development of low phytic acid cereals and legumes. The knockout of *OsMRP5* with myoinositol kinase gene (*OsMIK*) successfully reduced the phytic acid content in rice seeds (Tan et al., 2019). However, downregulating *TaABCC13* induced multiple developmental and functional phenotypes in wheat (*Triticum aestivum*), including reduced seed yields, altered stomatal movement, and altered root growth (Bhati et al., 2016). Phytic acid functions as a signaling factor and a precursor of other signaling factors as well; thus, it is not surprising that changes in its level cause developmental defects. Therefore, there is a need to generate agricultural products with low phytic acid contents without adversely affecting the plants.

Stress responses
ABC transporters are involved in plant responses to different types of stress by functioning as transporters of secondary

> **Box 1 APPLICATION POTENTIAL OF PLANT ABC TRANSPORTERS**
>
> - ABCC-induced sequestering of toxic heavy metals and metalloids into the vacuole could be exploited to produce plants that clean up or reduce the erosion of heavy metal-contaminated soils or crops containing fewer heavy metals.
> - Valuable secondary product yield could be increased by overexpressing ABC proteins that sequester these compounds in the vacuole.
> - The oil contents of oilseed plants and microalgae could be increased by genetic engineering using ABCA transporters similar to AtABCA9.
> - ABC transporters conferring pathogen resistance could be transferred to susceptible varieties to create pathogen-resistant plants.
> - Increasing the activities of ABC transporters that release compounds into the soil for symbiotic interactions could improve plant growth, as shown for strigolactone excretion.
> - Low phytic acid grains could be generated using a phytic acid transporter at the vacuole.
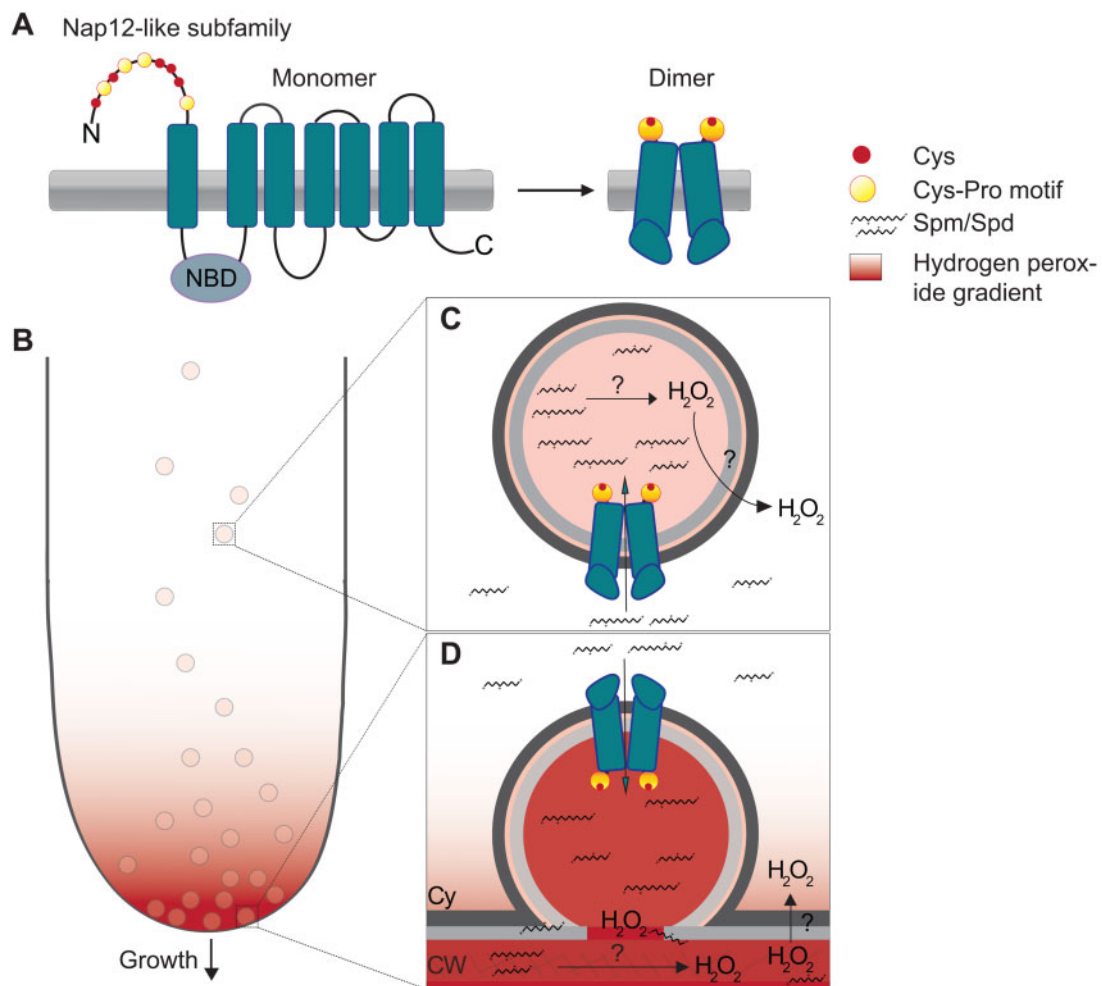

Figure 1 NAP12-like ABC proteins with many Cys residues at their N termini may be involved in the localized ROS generation required for tip growth. A, NAP12-like subfamily members possess a unique extracellular domain at their N termini, which is distinct from the other half-size ABCG transporters. The multiple Cys residues and Cys-proline) motifs in the extracellular domain are potential targets of ROS. B–D, Proposed mode of action of AtABCG28, a NAP12-like ABC transporter, in tip growth of a pollen tube and a root hair. AtABCG28 mediates the sequestration of the ROS precursor polyamines (spermine/spermidine [Spm/Spd]) from the cytosol (Cy) into secretory vesicles, which move and fuse to the growing tip (B). Spm/Spd is oxidized to generate H_2O_2 via enzymes present in secretory vesicles (C) and/or the cell wall (CW) after vesicle fusion (D). This process establishes tip-focused production of ROS, which is required for tip growth.

metabolites, xenobiotics, or stress hormones or as regulators of stress response genes. Throughout their lifetimes, plants are exposed to many host and non-host pathogens. Many pleiotropic drug resistance (PDR)-type ABC transporters serve as weapons that protect plants from pathogens by mediating the secretion of antimicrobial compounds. Therefore, pathogen resistance-associated PDRs are valuable genetic tools for generating pathogen-resistant crops. The representative one is wheat Lr34. The *Lr34res* allele is associated with durable resistance to rust diseases as well as powdery mildew (Krattinger et al., 2009). This allele is one of the long-lasting sources of quantitative fungal resistance in wheat. Heterologous expression of *Lr34res* confers disease resistance in maize (*Zea mays*), sorghum (*Sorghum bicolor*), and barley (*Hordeum vulgare*; Schnippenkoetter et al., 2017; Sucher et al., 2017; Boni et al., 2018). The expression of *Lr34res* in rice constitutively induced transcriptome changes similar to abscisic acid (ABA) responses, the *Lr34res* rice seedlings accumulated significantly higher levels of ABA than near-isogenic seedlings, and heterologously expressed Lr34 enhanced the accumulation of radioisotope-labeled ABA in yeast cells, suggesting that ABA is a substrate of Lr34 (Krattinger et al., 2019). Other reports suggest that Lr34 is involved in lipid transport and phenylpropanoid accumulation. Lr34 mediated the trans-leaflet movement of the phospholipids PA, PS, and PIs when expressed in tobacco (*Nicotiana tabacum*) Bright Yellow 2 cells (Deppe et al., 2018). A semi-targeted metabolomics analysis of flavonoid-rich wheat extracts revealed that the *Lr34res* allele accumulates much higher concentrations of phenylpropanoid diglyceride 1-*O*-*p*-coumaroyl-3-feruloylglycerol (CFG; Rajagopalan et al., 2020). CFG has low antifungal activity and might be a precursor of more efficient antimicrobial metabolites.

AtPEN3/AtPDR8/AtABCG36 is the most intensively studied pathogen resistance gene (Stein et al., 2006). The AtPEN3/AtPDR8/AtABCG36 transporter appears to be involved in transporting a broad range of substrates, including glucosinolate derivatives, auxin, and cadmium (Cd; Table 1). Camalexin was recently included in this potential substrate group (He et al., 2019). Another transporter also involved in camalexin secretion is AtABCG34/AtPDR6 (Khare et al., 2017). The *atabcg34/atpdr6* knockout mutant is sensitive to the fungus *Alternaria brassicicola* due to a decrease in the secretion of camalexin to the infected surface of the plant.

NpPDR1 was the first ABC protein to be identified for its antifungal effect as a sclareol exporter in *Nicotiana plumbaginifolia* (Stukkens et al., 2005). NpPDR1 orthologs in other *Nicotiana* species also function in pathogen resistance. *Nicotiana benthamiana* ABCG1/PDR1 and ABCG2/PDR2 are involved in capsidiol secretion during *Phytophthora infestans* infection (Shibata et al., 2016). *Nicotiana attenuata* PDR1 and PDR1-like function against infection by the fungus *Alternaria alternata* (Xu et al., 2018).

During plant responses to insect/herbivore attacks, ABC transporters are involved in the secretion of toxic compounds stored in glandular trichomes (secretory glands). NtPDR5/NtABCG5 was the first ABC protein reported to be involved in short- and long-term defense against insects by secreting toxic substrates (Bienert et al., 2012). NtPDR5/AtABCG5 is induced by wounding, methyl jasmonate (JA), or herbivory and is recruited to the damaged site of the plant. Silencing of *NtABCG5* supported the rapid growth of *Manduca sexta*, a common insect pest of Solanaceae. *Petunia hybrida* PDR2 is thought to be involved in trichome-related chemical defense against herbivores (Sasse et al., 2016). *PhPDR2* is highly expressed in trichomes and leaf margins, which are major sites of herbivore attack, and is induced upon insect attack. *PhPDR2*-downregulated plants exhibited enhanced susceptibility to *Spodoptera littoralis* and reduced concentrations of the potent insecticidal compounds petuniasterone and petuniolide.

Many structurally diverse molecules, including hormones, hormone derivatives, metal ions, phospholipids, and numerous secondary metabolites, have been suggested as potential substrates of plant PDRs mostly based on physiological data, as described above and elsewhere (Hwang et al., 2016). However, most of these putative substrates of plant PDRs have not been verified via direct transport assays because of the difficulties in expressing functional proteins in heterologous cell systems and also due to the chemical nature of some substrates (e.g. hydrophobicity). Many other candidate substrates of plant ABC transporters remain putative (Tables 1, 2), and it is largely unclear which are bona fide substrates of plant ABC proteins and which molecules undergo indirect changes in concentration due to the transport activity of ABC proteins. For example, the accumulation of CFG might be due to the transport activity of Lr34, or the changes in ABA distribution by Lr34 might have induced the synthesis of CFG.

Anthocyanins are a prominent group of pigments that function in stress responses and in interactions with other organisms. ABC transporters are important for anthocyanin accumulation in various species. In red grapevine (*Vitis vinifera*), VvABCC1 is expressed in the fruit epidermal layer during berry development. When expressed in yeast microsomes, VvABCC1 facilitated the uptake of the anthocyanin malvidin 3-*O*-glucoside in a glutathione-dependent manner (Francisco et al., 2013). Two ABC transporters of the saffron crocus (*Crocus sativus*), CsABCC4a and CsABCC2, facilitate the uptake of crocin into vacuoles in the stigma; this compound is primarily responsible for the red color of saffron (Demurtas et al., 2019). Expressing *CsABCC4a* together with *CCD2*, encoding an enzyme responsible for crocin production, resulted in the production of considerable levels of crocin in *N. benthamiana*, a plant that does not normally produce this compound. It is likely that the efficient transport of crocin into the vacuole reduces the

cytosolic concentrations of this product, resulting in the increased production of valuable secondary compounds by bypassing feedback inhibition.

Communication with other organisms

Some ABC transporters mediate communication between plants and other organisms by releasing chemicals from the root to the soil. These chemicals function as signals for symbiotic interactions and shape the root microbiome. ABC transporters play essential roles in the symbiosis of plants with arbuscular mycorrhizal fungi, which improve the acquisition of mineral nutrients. Mycorrhizal fungi and host plants exchange nutrients. The host plant provides sugars and fatty acids to support the growth of arbuscular mycorrhizal fungi, and the fungi provide nitrate and phosphate to the plant. Plants secrete strigolactone (SL) to initiate their interactions with their fungal partners, a process mediated by PDR1 in *P. hybrida* and *Petunia axillaris* (Solanaceae family; Kretzschmar et al., 2012; Sasse et al., 2015). PaPDR1 is polarly localized in hypodermal passage cells at the PM side facing the soil, where SL is released to the rhizosphere (Sasse et al., 2015). Increasing SL excretion via *PaPDR1* overexpression resulted in more rapid mycorrhization, providing an advantage to plants growing in phosphate-poor soils (Liu et al., 2018). In *M. truncatula* (Fabaceae family), MtABCG59 is a potential SL exporter that might facilitate mycorrhization (Banasiak et al., 2020).

STR and STR2 are half-size transporters of the ABCG subfamily that dimerize and specifically localize to the peri-arbuscular membrane (Zhang et al., 2010). STR-STR2, which are required for arbuscular mycorrhizal symbiosis in Medicago and rice (Zhang et al., 2010; Gutjahr et al., 2012), mediate the transfer of fatty acids from the host plant to the symbiont (Jiang et al., 2017).

Plants also communicate with other organisms via volatiles. Plant volatile organic compounds (VOCs) are often small, which led to the long-standing assumption that they passively diffuse into the environment. However, a recent study of *P. hybrida* flowers showed that VOC secretion depends on the half-size ABC transporter PhABCG1 (Adebesin et al., 2017). Downregulating *PhABCG1* resulted in decreased VOC emissions and an increase in internal VOC levels. Transport assays in tobacco BY-2 cells showed that PhABCG1 exports methylbenzoate and benzyl alcohol. The active transport of VOCs by ABC transporters protects the cell from the toxic effects of these compounds on the plasma membrane (PM).

Since secretion of chemicals by plant roots is important for formation of the root microbiome, and ABC proteins are often responsible for secretion of large organic molecules, we expect there will be more exciting new findings on ABC proteins involved in the root microbiome formation. Such information will allow us to develop tools to attract more beneficial bacteria and shape the root microbiome to protect plants against pathogens in a sustainable manner while improving yields.

Recent studies on ABCF and ABCI proteins

Some ABC proteins serve as regulators instead of transporters. ABCE and ABCF proteins only contain NBDs and, depending on their partner proteins, perform different functions such as regulation of protein synthesis and stability.

Plant ABCFs were initially assumed to function as ribosomal translation factors like their yeast orthologs, but recent studies revealed that they are involved in diverse cellular processes. AtGCN1/ABCF1 functions together with AtGCN20/AtABCF3 in translational regulation in response to pathogen infection (Izquierdo et al., 2018). AtABCF3 regulates the expression levels of aquaporins, which are involved in hydrogen peroxide (H_2O_2) transport (Li et al., 2018). AtABCF3 is also required for repairing DNA damage in roots (Han et al., 2018). AtGCN4/AtABCF4 might be involved in protein degradation (Kaundal et al., 2017). AtGCN4 interacts with RIN4 and 14-3-3 proteins, which activate proton pumps, and decreases their stability. As a result, proton pump activity decreases, which leads to stomatal closure, thereby resulting in increased drought tolerance and reduced pathogen entry through stomatal pores (Kaundal et al., 2017).

Malus domestica (apple) ABCF is localized to the pollen tube membrane, where it facilitates the entry of S-RNase into the pollen tube (Meng et al., 2014). Silencing of *MdABCF* reduced S-RNase uptake into pollen tubes, thereby weakening self-incompatibility. *Lilium regale* ABCF1 functions in pathogen responses via an unknown mechanism (Sun et al., 2016). *LrABCF1* is induced by viral infection, salicylic acid, and ethylene. Petunia plants heterologously expressing *LrABCF1* exhibited reduced susceptibility to Cauliflower mosaic virus, Tobacco rattle virus, and *Botrytis cinerea* infection.

AtNAP14/AtABCI11 is a chloroplast protein that is an Arabidopsis ortholog of cyanobacterial Fe transporters (Shimoni-Shor et al., 2010). *atabci11* plants exhibit an albino phenotype, growth defects, and increased accumulation of transition metals such as Fe and Mo, suggesting that AtABCI11 functions in transition metal homeostasis in plastids (Shimoni-Shor et al., 2010). OsABCI8 (recently renamed OsABCI7), a rice ortholog of AtABCI11, is thought to function in iron (Fe) homeostasis (Zeng et al., 2017). *osabci8* accumulates high concentrations of Fe, Ni, and Mn, but its albino phenotype appeared only after continuous exposure to rainy days. Arabidopsis ABCI10 shares overlapping functions with AtABCI11. *atabci10* plants are dwarf and albino, like *atabci11* plants. AtABCI10 localizes to the chloroplast inner envelope (IE) membrane, while AtABCI11 resides at the plastoglobuli. AtABCI10 interacts with AtABCI12, forming a complex at the IE, resembling group I energy-coupling factor-like ABC importers (Voith von Voithenberg et al., 2019).

Plant ABCIs have been implicated in transport of lipidic molecules into the chloroplast (TGD2 and TGD3) or metal ions into the chloroplast. A cluster of Arabidopsis ABCIs was recently implicated in the regulation of cytokinin responses (Kim et al., 2020). AtABCI19, AtABCI20, and AtABCI21, which clustered together in a phylogenetic tree, form a

300–400-kDa protein complex with unidentified endoplasmic reticulum (ER) membrane proteins. *abci20 abci21* double and *abci19 abci20 abci21* triple mutant seedlings exhibited enhanced sensitivity to cytokinin during root growth (Kim et al., 2020). Given that the cytokinin receptors and catabolic enzymes are prevalently localized to the ER and that cytokinin binding to the receptor is more favored at neutral-alkaline pH (as in the ER), the ER is likely an important site for cytokinin signaling and metabolism (Romanov et al., 2018) in addition to the PM (Antoniadi et al., 2020). Whether ABCI proteins are involved in cytokinin transport in or out of the ER is an intriguing question.

How do ABC transporters play such diverse roles in plants?

The incredibly diverse functions of plant ABC transporters described in the previous section and other reviews point to specific functional diversification mechanisms in addition to the expansion of ABC transporter gene family members. In this section, we introduce recent publications on plant ABC transporters, which describe mechanisms that make ABC transporters so versatile.

Dimerization with different partner ABC proteins

The Arabidopsis genome encodes 47 half-size ABC transporters (Verrier et al., 2008; Hwang et al., 2016), and it seems possible that some of them form dimers with multiple partners (Box 2). For example, AtABCG11 (WBC11) is a half-size transporter whose multiple dimerizing partners have been revealed: ABCG5, ABCG9, ABCG12, and ABCG14 (McFarlane et al., 2010; Le Hir et al., 2013; Lee et al., 2020). AtABCG11 appears to transport cuticular wax precursors to generate an intact cuticle layer on cotyledons by partnering with ABCG5 (Lee et al., 2020), precursors of the cuticular wax layer of stems by partnering with ABCG12 (McFarlane et al., 2010), and components required for vasculature development by partnering with ABCG9 or ABCG14 (Le Hir et al., 2013). Such diverse interactions with other ABC proteins might explain the broad range of growth and development defects observed in *abcg11* knockout plants (Panikashvili et al., 2010). Different gates and/or substrate binding pockets might be created when ABCG11 forms dimers with different partners. Thus, there is an exciting possibility that ABC transporters transport different compounds depending on their partner proteins. AtABCG16 is another half-size ABC protein that might form diverse transporters (Wang et al., 2019a, 2019b). AtABCG16 is involved in the transport of JA at the PM, jasmonoyl-isoleucine (JA-Ile) at the nuclear membrane (Li et al., 2017; Wang et al., 2019a, 2019b), and lipidic and/or phenolic precursors necessary for the formation of the intine and nexine layers of pollen (Yadav et al., 2014; Yim et al., 2016). However, the biochemical identification of partner proteins of AtABCG16 has not yet been performed; thus, it remains possible that the ABCG16 homodimer is responsible for the transport of multiple substrates.

Regulation of ABC transporters by protein phosphorylation and protein–protein interactions

Reversible post-translational modifications such as protein phosphorylation and protein–protein interactions regulate

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Box 2 DIFFERENTIAL PARTNERING OF HALF-SIZE ABC PROTEINS ENRICHES THE REPERTOIRE OF ABC TRANSPORTER FUNCTIONS

Functional ABC transporters require two TMDs and two NBDs. Half-size ABC proteins must dimerize to form functional ABC transporters. By binding with different partners, one half-size protein can form various functional transporters that translocate different substrates (see Box 2 Figure). The many half-size ABC proteins in plants further enrich the repertoire of functional transporters.
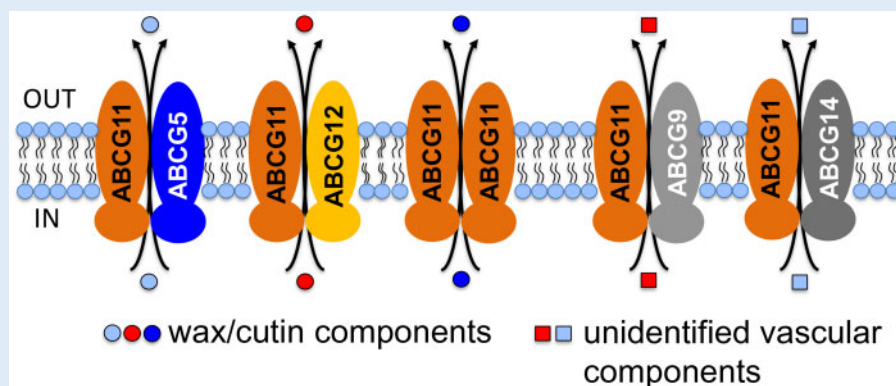
Box 2 Figure. *A. thaliana* ABCG11 homodimerizes or heterodimerizes with AtABCG5, AtABCG9, AtABCG12, or AtABCG14.

ABC transporter activity in many ways, such as turning its activity on/off, altering its protein stability, and binding with other proteins. TWISTED DWARF1 (TWD1), an immunophilin-like FKBP42, physically interacts with auxin-transporting ABCBs (Geisler and Hegedűs, 2020). TWD1 is a multidomain protein containing the conserved peptidylprolyl cis–trans isomerase (PPIase/FKBP) domain. Both *twd1* and *abcb1 abcb19* plants show reduced polar auxin transport, as well as dwarfism and twisted organs, suggesting that TWD1 plays an important role in ABCB-mediated auxin transport (Bouchard et al., 2006; Bailly et al., 2008). Extensive studies on TWD1 have suggested that it is important for protein biogenesis at the ER, trafficking to the PM, and transporting activity at the PM of auxin-transporting ABCBs (Aryal et al., 2016; Geisler and Hegedűs, 2020). In *twd1* Arabidopsis plants, ABCB1, ABCB4, and ABCB19 are trapped in the ER and then degraded (Wu et al., 2010; Wang et al., 2013; Aryal et al., 2016). Recently, a surface-exposed and conserved D/E-P motif has been identified in auxin-transporting ABCB proteins (Hao et al., 2020), which is located in the NBD in close proximity to the 12th TM helix involved in IAA binding (Bailly et al., 2011). Substitutions of either E^{1007} with A or P^{1008} with G in AtABCB1 significantly reduced the IAA transport activity in planta, the interaction with TWD1, and the TWD1-mediated regulation of transport activity, but not the basal ATPase activity or the PM localization of AtABCB1 (Hao et al., 2020). Therefore, a plausible scenario is that the conserved D/E-P motif may be an essential part of the TWD1 docking site on ABCBs and that the P residue of the D/E-P motif might be used to regulate ABCBs by PPIase activity, but this awaits experimental verification.

AtABCB19 and AtABCB1 are regulated by phosphorylation via the AGC kinases PHOTOTROPIN1 (phot1) and PINOID (PID), respectively (Christie et al., 2011; Henrichs et al., 2012). Phot1 kinase induces phosphorylation of AtABCB19, inhibiting the auxin transport activity of the ABCB, and thereby redirects auxin flow, leading to hypocotyl phototropism (Christie et al., 2011). The PID kinase affects the auxin transport activity of ABCB1 in a complex manner that depends on the presence of TWD1 (Henrichs et al., 2012; Wang et al., 2012). Co-expression of *PID* and *AtABCB1* in the absence of TWD1 induced phosphorylation of AtABCB1 and enhanced AtABCB1-mediated auxin efflux, whereas, in the presence of TWD1, co-expression of *PID* and *AtABCB1* abolished the auxin efflux activity of AtABCB1 (Henrichs et al., 2012).

Phosphorylation also regulates AtABCG36 activity. During plant responses to pathogens (pattern-triggered immunity and effector-triggered immunity), AtABCG36 (AtPDR8) is phosphorylated at multiple serine and threonine residues, which are clustered in its N terminus and central loop. Among these residues, the phosphorylation of Ser40 and Ser45 is critical for preventing penetration and subsequent haustorium formation in Arabidopsis leaves by the non-host barley powdery mildew pathogen *Blumeria graminis* f. sp. *hordei*. This phosphorylation does not affect the targeting of AtABCG36 to the penetration sites (Underwood and Somerville, 2017). Instead, it may regulate the transporter activity of AtABCG36, as these phosphorylation sites are located in the linker region, which is often the target of activity regulation in animal ABC proteins (Stolarczyk et al., 2011; Aryal et al., 2016). AtABCC1, another ABC member regulated by phosphorylation, detoxifies arsenic (As) by sequestering PC-As conjugates into the vacuole (Song et al., 2010; Zhang et al., 2017). Budding yeast expressing AtABCC1 in which Ser846 in the linker region between NBD1 and TMD2 was substituted with alanine exhibited reduced ABCC1-mediated resistance to As and decreased intracellular As content (Zhang et al., 2017). A phosphomimetic mutant study supported the notion that the phosphorylation of Ser846 is required for the role of AtABCC1 in As resistance.

Localization of ABC transporters to specific membrane regions

The polar localization of some ABC transporters to particular PM regions allows for the directional flow of phytohormones and the secretion of secondary metabolites. In petunia, the SL transporter PaPDR1 is polarly localized to the apical side of the PM in root tip cortex cells and to the outer lateral PM of hypodermal passage cells, facilitating the shootward movement, and secretion of synthesized SL, respectively (Kretzschmar et al., 2012; Sasse et al., 2015). Various Arabidopsis PDRs are specifically localized to the side of the PM facing outside the epidermal cells, where they likely function in secretion of cutin precursors (AtABCG32), the secondary metabolite camalexin for pathogen defense (AtABCG34 and AtABCG36), hormone precursors (AtABCG36), and root exudates for nutrient uptake (AtABCG37) into the environment (Strader and Bartel, 2009; Langowski et al., 2010; Bessire et al., 2011; Khare et al., 2017; Ziegler et al., 2017). The polar targeting of newly synthesized PDR proteins to a specific site of the PM is thought to underlie the asymmetric PM localization of PDRs, a process that involves actin cytoskeleton-dependent vesicle trafficking, Exo84b-mediated tethering, and vesicle fusion mediated by syntaxins such as PEN1 (Langowski et al., 2010; Mao et al., 2016). This mechanism involving the polar localization of PDRs differs from that of PIN auxin transporters, which are evenly targeted to the PM and subsequently recycled from specific sites of the PM.

Two rice ABCG transporters that are expressed in the tapetum appear to play different roles in the formation of surface protective layers due to their different localization patterns (Zhao et al., 2015). OsABCG26 is evenly localized at all sides of the PM of tapetal cells and is thought to be responsible for the transport of lipidic molecules from tapetal cells to anther wall layers. By contrast, OsABCG15 is polarly localized only to the locule side of the tapetal cell membrane and is responsible for the export of lipidic molecules for pollen exine development (Niu et al., 2013; Zhao et al., 2015; Chang et al., 2016).

Additional domains

The functional diversity of plant ABC transporters might be enhanced by the presence of extra domains. We recently reported a group of ABCG transporters with an extra domain at the N terminus that is enriched with cysteines (Cyss): NAP12-like ABCGs including AtABCG28 contain a long stretch at their N termini composed of a Cys-rich exoplasmic domain and an additional transmembrane segment next to the NBD (Do et al., 2019; Figure 1). These abundant Cyss might function in detecting the redox status of the environment and regulating the activity of NAP12-like ABCGs. It is tempting to speculate that, during the long evolution of ABC proteins, multiple gene fusion events added various extra domains to the basic skeleton of ABC proteins, thereby contributing to the diversity of their functions. This possibility is further discussed in the section "Evolution of ABC transporters in plants" of this review.

Alternative splicing

Alternative splicing is one of the many post-transcriptional regulatory mechanisms that enhance the plasticity and complexity of the transcriptome and proteome. Multiple splice variants have been reported for many plant ABC transporters. The Arabidopsis genome possesses 127 genes encoding ABC proteins, but 253 different alternatively spliced transcripts have been reported (TAIR annotated). A high percentage of alternatively spliced transcripts of ABC transporter genes contain premature termination codons. Most of these transcripts are degraded by nonsense-mediated mRNA decay and are not translated to produce proteins. Thus, alternative splicing might represent a mechanism to regulate the amounts of functional transcripts (Filichkin et al., 2010). However, some splice variants are predicted to introduce variations in the TM helixes or cytosolic parts of ABC proteins, thereby altering their binding partners, cellular localization, protein stability, activity level, or substrate selectivity (Chutkow et al., 1999; Ikeda et al., 2003; Gökirmak et al., 2016; Rehman et al., 2016; Seong et al., 2016; Zhang et al., 2020).

Evolution of ABC transporters in plants

ABC proteins are ancient and found in all organisms. These proteins evolved a dazzling array of structures and functions. Two key questions about the evolution of plant ABC proteins remain to be answered: How and why have plants evolved many more ABC proteins than other organisms; and how have plant ABC proteins evolved to transport such diverse molecules? The recent availability of the genome sequences of many plants has enabled the phylogenetic and evolutionary analysis of plant ABC genes. Such studies confirmed the previous observation that plant genomes generally contain many more ABC proteins, especially proteins in the ABCB and ABCG subfamilies (Andolfo et al., 2015), than most other organisms. Only a few species, including the spider mite *Tetranychus urticae* (103), the ciliate *Tetrahymena thermophila* (165), and some water molds (*Phytophthora ramorun*, 135, and *Phytophthora sojae*, 136), contain similar numbers of ABC proteins as plants. Perhaps this resulted from the many whole-genome multiplication (WGM) events in plant genomes and the preferential retention of ABC genes thereafter. Such preferential retention of ABC genes over other genes during gene loss after WGM might have been due to the strong connections of ABCs with other proteins. For example, in *Brassica rapa*, ABCGs function in the center of an interaction network and were therefore preferentially retained (Yan et al., 2017). According to the gene balance hypothesis, a gene encoding a component of a large protein complex, signaling network, or transcription network is more likely to be retained than a singleton, as its loss will lead to dangerous network imbalances. ABC genes might have evolved rapidly to acquire new functions to help plants to adjust to their new diverse environment on land (Yan et al., 2017). This idea is supported by the diverse functions performed by ABC proteins. These functions appear to help plants tolerate and proliferate in the land environment, which fluctuates more than the aqueous environment (Hwang et al., 2016). The usefulness of ABC proteins during the long history of evolution may lie in the fact that they use energy from ATP hydrolysis directly without requiring any other intervening steps. Thus, these proteins can function by themselves without the need for accompanying factors and can generate steeper concentration gradients compared with symporters and antiporters.

Our recent analysis of ABCG subfamily members in representative phyla of all organisms revealed that the full-size ABCG transporters explosively multiplied and differentiated in land plants and in the major plant pathogens oomycetes in a similar manner (Cho et al., 2019). Further analysis using systematic methods and laboratory experiments supported our idea that the ABCGs of these two interacting organisms coevolved: Plant ABCGs secrete secondary metabolites that protect them from pathogens, and pathogen ABCGs detoxify the secondary metabolites that permeate their cytosol. It is particularly interesting that the same ABCG subfamily transporters are used by both the host and its pathogens in this arms race. These transporters might have been selected because they are suitable for this type of chemical warfare. The internal needs of plants might also have contributed to the expansion of ABC transporters. For example, *AtABCC10* has eight orthologs in grapevine, likely because this diversity facilitates the vacuolar transport of the large variety of anthocyanins produced by this plant (Francisco et al., 2013).

In addition to clarifying the roles of the many ABC proteins in plants, an equally challenging question is how the ABC proteins evolved different structures that allow them to transport multiple, diverse substrates with no apparent chemical similarities. Multiple gene fusion events might have led to the evolution of ABC proteins from the simple structures found in prokaryotes to the more complex and complete structures found in eukaryotes (Xiong et al., 2015). During such fusion events, various combinations of ABC domains might have mixed and matched, which might have contributed to their diverse functions. However, this concept is currently merely a speculation. The recent

OUTSTANDING QUESTIONS

- What are the roles of the uncharacterized ABC transporters in Arabidopsis and rice?
- Which structural characteristics of plant ABC transporters allow them to recognize the diverse substrates that are unique to plants?
- Which compounds do ABC transporters release from the root to the soil, and how do they alter the root microbiome?
- How are ABC transporters regulated? How do the interactions between ABC transporters and partner proteins affect their substrate specificity? How do post-translational modifications such as phosphorylation, acetylation, N-glycosylation, lipidic modifications, ubiquitination, and sumoylation alter the functions/activity levels of ABC transporters?

development of cryo-EM technology will allow the structures of many ABCs to be determined, which could allow us to begin to answer this question. This new area of research on the evolution of ABC proteins should progress rapidly as many more genome sequences and advanced tools soon become available to facilitate the structural analysis of these large, complex proteins.

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