14-3-3 Proteins mediate the effects of certain protein kinases through their ability to bind well-defined phosphoserine or phosphothreonine containing peptide motifs (Muslin et al., 1996; Yaffe et al., 1997; Johnson et al., 2010), the coordination of which finally results in modification of the activity, stability, subcellular localization or interaction capability of the client protein (reviewed in Chevalier et al., 2009; Gökirmak et al., 2010). The fact that 14-3-3s form clamp-like dimers with each monomer capable of binding a phosphopeptide within an amphipathic groove (see Figure 1) immediately suggests that 14-3-3s function as an intermolecular bridge linking two different phosphoproteins. However, evidence that 14-3-3s act as adapters is surprisingly limited. More commonly, a 14-3-3 dimer seems to engage with two tandem phosphorylated sites in the same protein (Johnson et al., 2010).

Research in recent years has revealed an impressive list of putative 14-3-3 targets in both animals and plants (reviewed in MacKintosh, 2004; Chevalier et al., 2009; Oecking and Jaspert, 2009; Gökirmak et al., 2010; Denison et al., 2011; Johnson et al., 2011). The emerging picture is that 14-3-3s may function as dynamic coordinators of cellular responses to distinct signaling cues, due to their concerted regulation of cellular signaling, organization, and metabolism. In other words, depending on the environmental and cellular stimuli perceived by a cell, a specific subset of 14-3-3 clients become phosphorylated and — upon 14-3-3 association — brings about an integrated cellular response. Since 14-3-3 association normally relies on phosphorylation, such a scenario can in principle be achieved by 14-3-3 dependent regulation of almost all the substrates of particular kinases/phosphatases and/or of the kinases/phosphatases themselves.

Historically, plant 14-3-3s were thought to play a prominent role in primary metabolism (reviewed in Huber et al., 2002; Comparot et al., 2003; Denison et al., 2011) and ion homeostasis. Several recent high-throughput proteomic studies, however, have suggested them to also be key regulatory components in signaling cascades, in particular phytohormone mediated processes. Since some of these 14-3-3 interactions have already been reviewed (Chevalier et al., 2009; Oecking and Jaspert, 2009; Gökirmak et al., 2010; Denison et al., 2011) we will focus on recently identified putative interactors in Arabidopsis that represent the “historical” and “novel” 14-3-3 targets, namely transporters and proteins involved in hormonal signaling.

**DO 14-3-3s FINE-TUNE MEMBRANE TRANSPORT PROCESSES?**

While defined K⁺-channels (Sottocornola et al., 2006; Latz et al., 2007; Voelker et al., 2010) and the plasma membrane localized P-type H⁺-ATPase are among the “old players” in the Arabidopsis 14-3-3 field (reviewed in Oecking and Jaspert, 2009; Denison et al., 2011), recent studies have suggested a much wider diversity of target proteins involved in membrane transport processes than had previously been realized (Chang et al., 2009; Shin et al., 2011). **Table 1** summarizes these analyses, including data obtained via a yeast two-hybrid screen in our lab (Oecking et al., unpublished, see **Table A1** in Appendix). There are several exciting aspects that should be highlighted. The (putative) 14-3-3 clients include:
Almost 20 pumps belonging to the ATP-binding cassette (ABC) family (reviewed in Martinoia et al., 2002), the members of which can carry large organic molecules, including the phytohormone auxin.

Several carriers—some of which act as proton symporters [see (i)]—that permit the uptake of nutrients, such as phosphate, sulfate, carbohydrates, and ammonium.

A multitude of ion channels. Besides the “old players” mediating potassium transport, some poorly selective cation channels (cyclic nucleotide gated channel, CNGC), glutamate receptors which are implicated in cellular Ca²⁺ homeostasis [see (ii)] as well as voltage-dependent anion-selective channels (VDAC) may be subject to 14-3-3 regulation.

Finally some aquaporins (reviewed in Maurel et al., 2008) localized either in the plasma membrane (PIP) or the tonoplast (TIP) and known to facilitate the transport of water and/or gases, amongst others.

Taken together, this suggests that 14-3-3 proteins exert an impressively widespread influence on membrane transport processes in plants. Since plants are experts in maintaining optimal metabolic conditions under numerous environmental constraints, 14-3-3s may be the key to a tight and coordinated regulation of transporters that are directly or indirectly involved in ion and nutrient transport. Nevertheless, the number and diversity of these putative 14-3-3 clients are also somewhat intimidating and give rise to numerous questions. Which signals regulate which targets and which kinases are involved? Which mechanisms could elicit a concerted regulation of transporters whose interplay would make sense, such as proton-pumps and secondary active transporters? As the list of 14-3-3 clients is continually growing, the question whether the cellular “14-3-3 pool” is limiting under certain circumstances is becoming more important. However, it should be noted that, in the majority of cases, a mere handful of transporters has been identified. Indeed, the bulk of the above-mentioned clients was discovered by one study (Shin et al., 2011), suggesting that the given developmental stage and growth conditions of the plant material used favor 14-3-3 mediated regulation of membrane transporters.

ARE 14-3-3S GENERAL REGULATORS OF PHYTOHORMONE MEDIATED PROCESSES?

Meanwhile, Arabidopsis 14-3-3 proteins have been proved to be important mediators in signaling cascades (reviewed in Chevalier et al., 2009; Oecking and Jaspert, 2009; Gökirmak et al., 2010; Denison et al., 2011). This breakthrough was achieved by several elegant studies demonstrating 14-3-3s to be essential players in brassinosteroid (BR) signaling due to their modification of the subcellular localization of key transcription factors, such as brassinazole resistant1 (BZR1; Gampala et al., 2007; Ryu et al., 2007) and BRI1 EMS suppressor1 (BES1; Ryu et al., 2010). Currently available Arabidopsis 14-3-3 interactome data moreover suggest 14-3-3s to participate in processes mediated by almost any phytohormone (Chang et al., 2009; Paul et al., 2009; Shin et al., 2011; Swatek et al., 2011; summarized in Table 2 which includes data obtained via a yeast two-hybrid screen in our lab; Oecking et al., unpublished, see Table A1 in Appendix). First of all, not only a multitude of further proteins likewise involved in BR signaling but also polypeptides critical for its biosynthesis have been identified as potential 14-3-3 clients. A comparable scenario emerges with respect to the gaseous hormone ethylene (Table 2). At present, we can only speculate as to why multiple 14-3-3 interactions might be required to control a defined cellular response. One conceivable
Table 1 | A summary of prominent membrane transporters recently identified as putative *Arabidopsis* 14-3-3 interactors.

| Category of transporter | Putative 14-3-3 client | Transported molecule | Detection of interaction | Reference |
|-------------------------|-------------------------|----------------------|--------------------------|-----------|
| **PUMP**                |                         |                      |                          |           |
| P-type ATPase           | AHA1, AHA2              | H⁺                   | Y2H                      | Oecking et al. (unpublished) |
|                         | AHA2                    |                      |                          | Arabidopsis Interactome Mapping Consortium (2011) |
|                         | AHA2, AHA3, AHA10       |                      |                          | Shin et al. (2011) |
|                         | AHA6                    |                      |                          | Chang et al. (2009), Arabidopsis Interactome Mapping Consortium (2011) |
|                         | ACA2, ECA1, ECA2        | Ca²⁺                 | AC                       | Shin et al. (2011) |
|                         | HMA4                    | Heavy metals         | TAP, Y2H                 | Chang et al. (2009), Arabidopsis Interactome Mapping Consortium (2011) |
| V-type ATPase           | HMA6, HMA7              |                      | AC                       | Shin et al. (2011) |
|                         | VHA-A, VHA-B2           | H⁺                   | AC                       | Oecking et al. (unpublished) |
|                         | VHA-H                   |                      | Y2H                      | Arabidopsis Interactome Mapping Consortium (2011) |
| H⁺-PPase                | AVP1                    | H⁺                   | Y2H                      | Oecking et al. (unpublished) |
|                         | AVP2                    |                      | AC                       | Shin et al. (2011) |
| ABC transporter         | 20 Isoforms belonging to subgroups A, B, C, or G | Organic molecules | AC                       | Shin et al. (2011) |
| **CARRIER**            |                         |                      |                          |           |
| H⁺-symporter            | SUC6, TMT1, STP14       | Carbohydrates        | AC                       | Shin et al. (2011) |
|                         | STP4                    |                      | Y2H                      | Oecking et al. (unpublished) |
|                         | SULTR1;3, SULTR2;1, SULTR3;1, SULTR4;1 | SO₄²⁻ | AC                       | Shin et al. (2011) |
|                         | PHT1;1, PHT1;6          | PO₄³⁻                 | AC                       | Oecking et al. (unpublished) |
|                         | PHT3;1                 |                      | Y2H                      | Arabidopsis Interactome Mapping Consortium (2011) |
| Facilitator             | CAX2                    | Ca²⁺                 | AC                       | Shin et al. (2011) |
|                         | AMT1;1                 | NH₄⁺                 | AC                       | Oecking et al. (unpublished) |
|                         | COPT1                  | copper               | Y2H                      | Arabidopsis Interactome Mapping Consortium (2011) |
|                         | KUP6, KUP7             | K⁺                   | AC                       | Shin et al. (2011) |
|                         | MGT2                   | Magnesium            | Y2H                      | Shin et al. (2011) |
|                         | ZIP10                  | Zinc                 | AC                       | Shin et al. (2011) |
| **CHANNEL**            |                         |                      |                          |           |
| Tandem pore K⁺ channel  | TPK1, TPK3             | K⁺                   | GST-PD, SPR              | Latz et al. (2007) |
|                         | TPK1, TPK5             |                      | AC                       | Shin et al. (2011) |
| Shaker K⁺ channel       | KAT1                   | K⁺                   | Y2H, BiFC               | Voelker et al. (2010) |
|                         | AKT2, AKT5             |                      | In vitro overlay         | Sottocornola et al. (2006) |
|                         | GORK                   |                      | AC                       | Shin et al. (2011) |
|                         |                       |                      | TAP, Y2H                 | Chang et al. (2009), Arabidopsis Interactome Mapping Consortium (2011) |
| Cyclic nucleotide gated channel (CNGC) | Isforms 5, 6, 10, 18 | Cations             | AC                       | Shin et al. (2011) |
|                         | isoform 17             |                      | Y2H                      | Oecking et al. (unpublished) |
| Glutamate receptor      | Seven different isoforms | Ca²⁺?               | TAP, Y2H, AC             | Chang et al. (2009), Arabidopsis Interactome Mapping Consortium (2011), Shin et al. (2011) |
| Voltage-dependent anion channel | VDAC1, VDAC2, VDAC3 | Anions               | Y2H                      | Oecking et al. (unpublished) |
| Aquaporin               | PIP1;1, PIP1;5, PIP2;7, TIP1;2, TIP2;1 | H₂O, gases          | Y2H                      | Oecking et al. (unpublished) |

AC, 14-3-3 affinity chromatography of plant extracts; BiFC, bimolecular fluorescence complementation; PD, pull-down assay; SPR, surface plasmon resonance; TAP, tandem affinity purification of 14-3-3 protein complexes; Y2H yeast two-hybrid.
Table 2 | A summary of recently identified putative *Arabidopsis* 14-3-3 interactors involved in phytohormone signaling or biosynthesis.

| Hormone pathway | Putative 14-3-3 client | Client's function | Detection of interaction | Reference |
|-----------------|-------------------------|------------------|--------------------------|-----------|
| BR signaling    | BRI1, BRL2, BAK1        | Receptor/co-receptor | TAP, Y2H                | Chang et al. (2009), *Arabidopsis* Interactome Mapping Consortium (2011) |
|                 | SERK1                   |                  | Co-IP, Y2H              | Karlova et al. (2006), *Arabidopsis* Interactome Mapping Consortium (2011) |
|                 | BSU1, BSL1              | Protein phosphatase | TAP, Y2H                | Chang et al. (2009), *Arabidopsis* Interactome Mapping Consortium (2011) |
|                 | BZR1                    | Transcriptional regulator | BiFC, Y2H            | Gampala et al. (2007), Ryu et al. (2007), *Arabidopsis* Interactome Mapping Consortium (2011) |
|                 | BES1                    |                  | Co-IP, Y2H              | Ryu et al. (2010), *Arabidopsis* Interactome Mapping Consortium (2011) |
| BR biosynthesis | BEE3, BES1, BIM1, BZR1  |                  | Y2H                     | Oecking et al. (unpublished) (see Table A1 in Appendix) |
|                 | CYP85A19                | BR-6-oxidase      | AC                      | Shin et al. (2011) |
| Ethylene signaling | CBPath1/DWF1          | Campesterol formation | Y2H                    | Oecking et al. (unpublished) (see Table A1 in Appendix) |
|                 | ETR1                    | Receptor          | AC                      | Shin et al. (2011) |
|                 | EIN2                    | Membrane protein  | AC                      | Shin et al. (2011) |
|                 | ERF1, ERF9              | Transcriptional regulator | AC                  | Shin et al. (2011) |
|                 | ERF11                   |                  | Y2H                     | Oecking et al. (unpublished) (see Table A1 in Appendix) |
| Ethylene biosynthesis | ACS6, ACS7, ACS8       | ACC-synthase      | TAP, Y2H                | Chang et al. (2009), *Arabidopsis* Interactome Mapping Consortium (2011) |
|                 | ACS6, ACS10             |                  | AC                      | Shin et al. (2011) |
|                 | ACO2, ACO4              | ACC-oxidase       | AC                      | Oecking et al. (unpublished) (see Table A1 in Appendix) |
|                 | EOL1, EOL2              | ETO1-like: direct ACS for degradation | TAP, Y2H | Chang et al. (2009), *Arabidopsis* Interactome Mapping Consortium (2011) |
|                 | EOL2                    |                  | AC                      | Shin et al. (2011) |
| ABA signaling   | ABF1, ABF2, ABF3, ABF4, | Transcriptional regulator | Y2H                    | Oecking et al. (unpublished) (see Table A1 in Appendix) |
|                 | ABF5, AREB3             |                  |                        |                        |
| GA signaling    | RGA, RGL2               | Transcriptional regulator | AC                      | Shin et al. (2011) |
| CK signaling    | ARR12                   | Transcriptional regulator | AC                      | Shin et al. (2011) |
|                 | ARR2                    |                  | Y2H                     | *Arabidopsis* Interactome Mapping Consortium (2011) |
|                 | CRF6                    |                  | Y2H                     | Oecking et al. (unpublished) (see Table A1 in Appendix) |
| CK homeostasis  | CXX3                    | CK oxidase        | AC                      | Shin et al. (2011) |
| Auxin signaling | ARF6, ARF15, ARF18      | Transcriptional regulator | AC                      | Shin et al. (2011) |
|                 | IAA14, IAA17, IAA18, IAA19 |               | AC                      | Shin et al. (2011) |
| Auxin homeostasis | NIT1, NIT2             | Nitrilase         | AC                      | Paul et al. (2009) |
|                 | NIT1                    |                  | Y2H                     | Oecking et al. (unpublished) (see Table A1 in Appendix) |
|                 | NIT3                    |                  | AC                      | Shin et al. (2011) |
|                 | GH3.3, GH3.5            | IAA amido synthetase | AC                     | Shin et al. (2011) |
|                 | GH3.9                   |                  | AC                      | Swatek et al. (2011) |
|                 | IAR4                    | IAA-conjugate resistant | AC                     | Shin et al. (2011) |

AC, 14-3-3 affinity chromatography of plant extracts; BiFC, bimolecular fluorescence complementation; Co-IP, co-immunoprecipitation; TAP, tandem affinity purification of 14-3-3 protein complexes; Y2H, yeast two-hybrid.

...scenario is that 14-3-3 function as molecular gauges, thereby forcing the cell to react to a given phytohormone according to the signal strength. Taking into account that clients involved in several cellular processes might compete for binding to 14-3-3s, numerous targets within one defined pathway are assumed to channel the overall cellular response.

Remarkably, the modification of transcriptional regulators involved in hormonal signaling seems to be another hotspot in *Arabidopsis* 14-3-3 biology. In this regard, several prominent proteins, which act as either repressors or activators of gene expression in BR (BZR1, BES1, BIM1), ethylene [ethylene responsive factor (ERF)], auxin [auxin/indole-3-acetic acid proteins (Aux/IAA),
auxin response transcription factor (ARF)], gibberellin (GA) [repressor of GA1-3 (RGA), RGA-like (RGL)], abscisic acid (ABA) [ABA response element binding factor (ABF)], and cytokinin (CK) [Arabidopsis response regulator (ARR), cytokinin response factor (CRF)] responses, are among the putative 14-3-3 clients in Arabidopsis (Table 2). In contrast to BZR1/BES1, which are retained in the cytosol upon 14-3-3 association (Gampala et al., 2007; Ryu et al., 2007, 2010), the members of the ABF subfamily of BASIC REGION/LEUCINE ZIPPER (bZIP) transcription factors constitutively localize to the nucleus, as shown for ABA INSENSITIVE 5 (ABI5; Lopez-Molina et al., 2002), ABF3 (Sirichandra et al., 2010) and the rice homolog OREB1 (Hong et al., 2011).

In this respect, 14-3-3s have been proposed to be critical for the stability of the ABF3 protein, the proteasomal turnover rate of which is high in the absence of ABA and 14-3-3s (Sirichandra et al., 2010). Even though 14-3-3-dependent modification of transcriptional regulators mediating ethylene, auxin, GA, and CK responses has yet to be verified, 14-3-3s might in summary be far more important for assuring the developmental plasticity of plants than has yet been assumed. The fact that more and more proteins are identified as putative targets moreover implies that 14-3-3 interactions are highly dynamic which would enable the cellular 14-3-3 “pool” to immediately and precisely react to altered signaling cues.

14-3-3s ARE CRITICAL FOR FLORAL TRANSITION IN RICE

While global studies are essential to get an impression of the extent of the plant 14-3-3 interactome, the necessity to address the biological significance of individual interactions is more pressing than ever. In this respect, a recent study elegantly combining biochemistry, cell biology, and genetics has impressively proved 14-3-3s to be essential components of the florigen activation complex (FCA) that promotes flowering in the short day plant rice (Taoka et al., 2011). The term “florigen” was created in 1936 and refers to a molecule that is generated in leaves under inductive photoperiodic conditions and subsequently transported to the shoot apex (Chailakhyan, 1936). Evidence could only recently be provided that the protein flowering locus T (FT) represents such a long-distance signal in the facultative long day plant Arabidopsis (Mathieu et al., 2007). In the shoot apex, a complex of FT and the bZIP transcription factor flowering locus D (FD) initiates floral development through transcriptional activation of floral identity genes (Abe et al., 2005; Wigge et al., 2005).

Using the rice FT homolog Hd3a as a bait in a yeast two-hybrid screen, (Taoka et al., 2011) identified rice 14-3-3 isoforms as well as OsFD1, a rice homolog of the Arabidopsis FD, as putative binding partners. The initially astonishing observation that Hd3a is unable to interact directly with OsFD1 gave rise to subsequent in-depth analyses demonstrating 14-3-3s to mediate this interaction. Remarkably, the binding sites in 14-3-3 for Hd3a and OsFD1 are separated, indicating that the two partners bind in different manner. OsFD1 represents the typical 14-3-3 target, in that its coordination within the typical groove of a 14-3-3 monomer depends on phosphorylation. However, in contrast with most physiological targets, Hd3a does not have to be phosphorylated in order to associate with 14-3-3s. The obtained crystal structure of the Hd3a:14-3-3 complex revealed a fascinating difference as compared to the canonical 14-3-3 interactions: an unphosphorylated Hd3a monomer binds “on top” of each 14-3-3 monomer, thus extending the W-shaped structure of the 14-3-3 dimer (Taoka et al., 2011; Figure 1). Crystal soaking in the presence of a phosphorylated OsFD1 peptide representing the 14-3-3 binding site finally allowed the modeling of the FCA holocomplex composed of 14-3-3, OsFD1 and Hd3a. Notably, even though 14-3-3s mediate the Hd3a:OsFD1 interaction, the two proteins do not come in contact with each other, suggesting 14-3-3s to function as a platform enabling spatial proximity but not direct linkage (Taoka et al., 2011). On the basis of cell biological data Taoka et al. (2011) proposed a model according to which 14-3-3s act as cytoplasmic receptors for the “florigen” Hd3a in the shoot apex. Once this protein couple enters the nucleus, a ternary complex including phosphorylated OsFD1 is built, which in turn is retained in the nucleus and activates transcription of genes crucial for floral induction. Finally, several experiments performed with mutant versions of either Hd3a or OsFD1 that had lost their ability to interact with 14-3-3s have impressively proved the in vivo significance of 14-3-3 association for flowering in rice.

However, based upon the current structural knowledge nearly each 14-3-3 client should be able to associate with the Hd3a:14-3-3 complex. Thus, one crucial question is still unanswered: what determines specificity of the Hd3a:14-3-3 complex to interact exclusively with OsFD?

MINOR KNOWLEDGE ABOUT THE BIOLOGICAL ROLE OF DISTINCT 14-3-3 ISOFORMS

The above-mentioned studies, demonstrating that 14-3-3s are of the utmost importance for BR signaling and timing of floral transition, were focused on particular 14-3-3 client proteins and have generated substantial insight into the function of plant 14-3-3s. Considering the enormous quantity and functional complexity of the recently identified putative 14-3-3 targets, the subset of which may vary considerably as a function of the developmental and physiological stage, the question as to whether Arabidopsis 14-3-3 mutants can broaden our understanding of 14-3-3 function becomes more and more critical. Arabidopsis expresses thirteen 14-3-3 isoforms that can be divided into two major phylogenetic groups, the epsilon and the non-epsilon group, the latter consisting of three organizational subgroups. Since the epsilon group is considered to harbor living fossil isoforms which may fulfill fundamental eukaryotic functions, non-epsilon members may be responsible for organism-specific regulatory aspects.

The current knowledge about plants characterized by reduced or absent expression of specific 14-3-3 isoforms is limited (see Oecking and Jaspert, 2009; Denison et al., 2011). We identified T-DNA induced loss-of-function alleles of several individual non-epsilon 14-3-3 isoforms, which collectively do not show a statistically significant phenotype under normal growth conditions. The same applies to the simultaneous loss-of-function of two 14-3-3 isoforms (kappa/lambda) constituting a phylogenetic non-epsilon subgroup, suggesting functional redundancy among members of the non-epsilon group at least with respect to fundamental functions (data not shown). Beyond that, although lambda and kappa were the most frequently 14-3-3 isoforms identified
in a yeast two-hybrid screen to interact with BZR1, the corresponding double knockout mutants did not display altered BR responses (Gampala et al., 2007). Taken together, redundancy of all non-epison isoforms independent of their belonging to different phylogenetic subgroups is likely. Thus, higher order loss-of-function mutants seem to be required to produce a phenotype, which in turn is expected to be pleiotropic and is thus difficult to interpret. Nevertheless, focusing on well-defined developmental stages could provide hints for the dominant and major 14-3-3 targets under the given circumstances.

What about epsilon group members? While many of the recent proteome wide approaches in Arabidopsis have focused on the identification of putative non-epison 14-3-3 interactors, only one study compared two phylogenetically distinct isoforms (Swatek et al., 2011). The results suggest not only isoform specificity of several target proteins but also preference for 14-3-3 dimer formation between phylogenetically similar 14-3-3 isoforms. Hence, functional specialization may exist, at least between members of the non-epison and epsilon group.

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### APPENDIX

Table A1 | Results of a yeast two-hybrid screen using a cDNA library obtained from 3 days old etiolated Arabidopsis seedlings (Kim et al., 1997) and different Arabidopsis 14-3-3 isoforms as a bait.

| Locus | Gene name |
|-------|-----------|
| **MEMBRANE TRANSPORTER** | |
| AT1G15690 | H^+^-translocating inorganic pyrophosphatase (H^+^-PPase) located in the vacuolar membrane (AVP1) |
| AT2G18960 | Plasma membrane H^+^-ATPase1 (AHA1) |
| AT2G45960 | Plasma membrane intrinsic protein (PIP1;2) |
| AT3G01280 | Voltage-dependent anion channel 1 (VDAC1) |
| AT3G16240 | Tonoplast intrinsic protein (TIP2;1) |
| AT3G19930 | Sucrose hydrogen symporter, sugar transporter 4 (STP4) |
| AT3G26520 | Tonoplast intrinsic protein (TIP1;2) |
| AT3G42050 | Vacuolar ATPsynthase subunit H family protein (VHA-H) |
| AT4G30360 | Cyclic nucleotide gated channel 17 (CNGC17) |
| AT4G30190 | Plasma membrane H^+^-ATPase2 (AHA2) |
| AT4G35100 | Plasma membrane intrinsic protein (PIP2;7) |
| AT5G14040 | Phosphate transporter (PHT3;1) |
| AT5G15090 | Voltage-dependent anion channel (VDAC3) |
| AT5G69030 | Copper transporter 1 (COPT1) |
| AT5G67500 | Voltage-dependent anion channel 2 (VDAC2) |
| **HORMONE SIGNALING/BIOSYNTHESIS** | |
| AT1G05010 | ACC-oxidase 4 (ACO4)/ethylene forming enzyme (EFE) |
| AT1G19350 | BRI1-EMS-suppressor 1 (BES1)/brassinazole-resistant 2 (BZR2) |
| AT1G28370 | Ethylene response factor 11 (ERF11) |
| AT1G45249 | Abscisic acid responsive elements-binding factor 2 (ABF2) |
| AT1G49720 | Abscisic acid responsive elements-binding factor 1 (ABF1) |
| AT1G62380 | ACC-oxidase 2 (ACO2) |
| AT1G73830 | BR enhanced expression 3 (BEE3) |
| AT1G75080 | Brassinazole-resistant 1 (BZR1) |
| AT2G36270 | Abscisic acid insensitive 5 (ABI5) |
| AT3G19290 | Abscisic acid responsive elements-binding factor 4 (ABF4) |
| AT3G19820 | Cabbage 1 (CB81)/dwarf 1 (DWF1) |
| AT3G44310 | Nitrilase 1 (NIT1) |
| AT3G56850 | Abscisic acid responsive element binding protein 3 (AREB3) |
| AT3G61630 | Cytokinin response factor 6 (CRF6) |
| AT4G34000 | Abscisic acid responsive elements-binding factor 3 (ABF3) |
| AT5G08130 | BES1-interacting Myc-like protein 1 (BIM1) |

Shown are putative 14-3-3 interactors involved in either membrane transport processes or phytohormone signaling/biosynthesis.