Biochemical and Biophysical Research Communications 445 (2014) 54–57

Contents lists available at ScienceDirect

Biochemical and Biophysical Research Communications

journal homepage: www.elsevier.com/locate/ybbrc

Arabidopsis G-protein β subunit AGB1 interacts with NPH3 and is involved in phototropism

Jeeraporn Kansup [a], Daisuke Tsugama [a,b,1], Shenkui Liu [c], Tetsuo Takano [a,*]

[a] Asian Natural Environmental Science Center, The University of Tokyo, Nishitokyo, Tokyo 188-0002, Japan
[b] Laboratory of Plant Molecular Genetics, Graduate School of Agricultural and Life Sciences, University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan
[c] Alkali Soil Natural Environmental Science Center, Northeast Forestry University, Harbin 150040, China

ARTICLE INFO

Article history:
Received 17 January 2014
Available online 31 January 2014

Keywords:
Arabidopsis
Heterotrimeric G protein β subunit
Nonphototropic hypocotyl 3
Protein–protein interaction
Phototropism

ABSTRACT

Heterotrimeric G proteins (Gα, Gβ and Gγ) have pleiotropic roles in plants, but molecular mechanisms underlying them remain to be elucidated. Here we show that Arabidopsis Gβ (AGB1) interacts with NPH3, a regulator of phototropism. Yeast two-hybrid assays, *in vitro* pull-down assays and bimolecular fluorescence complementation assays showed that AGB1 and NPH3 physically interact. NPH3-null mutation (*nph3*) is known to completely abolish hypocotyl phototropism. Loss-of-function mutants of AGB1 (*agb1-1* and *agb1-2*) showed decreased hypocotyl phototropism, and *agb1*/*nph3* double mutants showed no hypocotyl phototropism. These results suggest that AGB1 is involved in the NPH3-mediated regulation of phototropism.

1. Introduction

Heterotrimeric G-proteins (Gα, Gβ, and Gγ) are signaling molecules found in a variety of eukaryotic organisms. They mediate extracellular signals perceived by G-protein-coupled receptors (GPCRs) to intracellular effectors, and are involved in diverse cellular processes. Gβ of Arabidopsis (AGB1) is involved in regulating morphology and sensitivities to various stimuli ([1], for a review). Previous studies showed that AGB1 interacts with a Golgi-localized hexose transporter, SGB1 [2], a regulator of auxin transport, NDL1 [3], an ethylene biosynthesis-related protein, ARD1 [4], and many proteins involved in cell wall modification [5]. However, the molecular mechanisms underlying AGB1-mediated signaling are still unclear.

We previously performed a yeast two-hybrid screen using AGB1 as bait [6], and identified several putative AGB1-interacting proteins [6–9]. One of these proteins is NPH3 (Nonphototropic hypocotyl 3), which interacts with a blue light receptor, phot1 [10,11], and regulates phototropic responses [10,12] and leaf blue light responses [13]. *NPH3* has two transcript variants, *NPH3.1* and *NPH3.2*. NPH3.2 corresponds to the C-terminal region-truncated version of NPH3.1. NPH3.1 consists of N-terminal BTB domain, central NPH3 domain and C-terminal coiled-coil domain [14]. The coiled-coil domain of NPH3.1 interacts with phot1 [10], and the BTB domain interacts with CULLIN3 (CUL3), a scaffold protein for ubiquitin ligase complex [15]. Both of these interactions are involved in regulating the NPH3-mediated blue light responses [10,15].

Arabidopsis G proteins have been suggested to play roles in light responses. For example, blue light-induced phenylalanine production in etiolated seedlings is impaired in an Arabidopsis Gα (GPA1)-null mutant *gpa1-3* [16]. Another GPA1-null mutant, *gpa1-4*, and an AGB1-null mutant, *agb1-2*, are both less sensitive to blue light and far-red light in seed germination [17]. *gpa1-4* is less sensitive to the cell death mediated by a red light receptor, phyA, while *agb1-2* is more sensitive to the phyA-mediated cell death [18]. However, it is unclear whether G proteins are involved in the phototropic responses mediated by phot1 and NPH3.

Here we show that AGB1 physically interacts with NPH3 and is involved in the NPH3-dependent phototropic responses.

2. Materials and methods

2.1. Plant material, growth conditions and analysis of phototropism

Arabidopsis thaliana ecotype Columbia-0 (Col-0) was used throughout the experiments. Seeds of *nph3-7* (SALK_110039), *nph3-8* (CS322676), *agb1-1* (CS3976) [19] and *agb1-2* (CS6536)

* Corresponding author. Fax: +81 42 463 1618.
E-mail addresses: jeerapornk@anesc.u-tokyo.ac.jp (J. Kansup), tsugama@anesc.u-tokyo.ac.jp (D. Tsugama), shenkuiliu@nefu.edu.cn (S. Liu), takano@anesc.u-tokyo.ac.jp (T. Takano).
[1] Present address: Biology Department, 208 Mueller Laboratory, Pennsylvania State University, University Park, PA 16802, USA.

http://dx.doi.org/10.1016/j.bbrc.2014.01.106
0006-291X/

[20] were obtained from the Arabidopsis Biological Research Center (ABRC). For SALK_110039 and CS322676, T-DNA insertion was confirmed by genomic PCR analysis (Supplementary Fig. S1A and B). Primers used for the genomic PCR analysis are shown in Supplementary Table S1.

Seeds were surface sterilized and sown on 0.8% agar medium containing 0.5× Murashige and Skoog (MS) salts (Wako), 1% (w/v) sucrose and 0.5 g/L MES, pH 5.8, chilled at 4 °C in the dark for 3 d (stratified), and germinated at 22 °C. Plants were grown at 22 °C under 16-h-light/8-h-dark photoperiod for RT-PCR and genomic PCR analyses. To measure phototropic curvature, plants were grown for three days in the dark and were irradiated with unilateral blue light for 20 h [21].

2.2. Yeast two-hybrid (Y2H) analysis

pBluescript II SK⁻ NPH3.1, which contains full-length *NPH3.1* (see Supplementary Method S1), was digested by *Eco*RV and *Sac*I, and the resultant fragment containing the 3′ region (the position 1546-2241 from the start codon) of the open reading frame (ORF) of *NPH3.1* was inserted into the *Sma*I-*Sac*I site of pGADT7-Rec, generating pGAD-NPH3.1C. pBluescript II SK⁻ NPH3.1 (see Supplementary Method S1) was digested by *Eco*RI and *Xba*I, and the resultant fragment containing the full-length ORF of *NPH3.1* was inserted into the *Eco*RI-*Xba*I site of pGADT7-Rec, generating pGAD-NPH3.1. pGBK-AGB1 [6] and each pGAD construct were co-introduced into the *Saccharomyces cerevisiae* strain AH109. Reporter gene activation in the transformed yeast cells was examined by growing them on the SD (synthetic dextrose) medium lacking histidine and adenine as previously reported [6].

2.3. In vitro pull-down assay

To express GST-fused NPH3 variants in *Escherichia coli*, the ORFs of *NPH3.1*, *NPH3.2* and their truncated versions were inserted into pGEX-5X-1, generating pGEX-5X-NPH3.1, pGEX-5X-NPH3.2, pGEX-5X-BTB+I+II and pGEX-5X-III+IV, as described in Supplementary Method S1. These constructs were transformed into the *E. coli* strain BL21 (DE3), and transformed cells were cultured at 37 °C in LB medium until OD_{600} reached 0.5. IPTG was then added to the medium at 0.5 mM final concentration (for pGEX-5X-NPH3.1 and pGEX-5X-NPH3.2) or 0.3 mM final concentration (for pGEX-5X-BTB+I+II and pGEX-5X-III+IV), and the cells were further cultured at 28 °C for 4 h (for pGEX-5X-NPH3.1 and pGEX-5X-NPH3.2) or 3 h (for pGEX-5X-BTB+I+II and pGEX-5X-III+IV). The cells were then harvested by centrifugation and resuspended in 1× PBS (phosphate-buffered saline: 137 mM NaCl, 8.10 mM $Na_2HPO_4 \cdot 12H_2O$, 2.68 mM KCl, 1.47 mM KH_2PO_4, pH 7.4) with 2 mg/ml lysozyme (Wako). The cell suspension was frozen at −80 °C and thawed at room temperature. Freezing and thawing were repeated two more times to lyse the cells, and two units of recombinant DNase I (Takara) was added to the solution. The solution was incubated at room temperature until the solution became fluid due to DNA degradation. The solution was then centrifuged at 12 000*g* for 5 min and the supernatant was used as crude extracts. The presence of the GST-fused proteins in the crude extracts was confirmed by Western blotting using a goat anti-GST antibody (GE Healthcare) and a horseradish peroxidase (HRP)-conjugated rabbit anti-goat IgG antibody (MBL).

GST-fused proteins in the crude extracts were bound to Glutathione Sepharose 4 Fast Flow (GE Healthcare) following the manufacturer's instructions, and the resin was washed 4 times by 1× PBS. The resin was then resuspended in a solution containing purified polyhistidine-tagged AGB1 (His-AGB1), which was prepared as previously described [6], and incubated at room temperature for 60 min with gentle shaking. The resin was then washed 4 times by 1× PBS, resuspended in 20 mM reduced glutathione in 50 mM Tris–HCl, pH 8.0, and incubated at room temperature for 15 min to elute the GST-fused proteins. The slurry of the resin was centrifuged for 3 min at 12 000*g*, and His-AGB1 in the supernatant was analyzed by Western blotting using HisProbe-HRP (Thermo Fisher Scientific). When used, HisProbe-HRP was diluted 2000 times by 1× PBS. Signals were detected with SuperSignal West Pico Chemiluminescent Substrate (Thermo Fisher Scientific) and the Las 1000 image analyzer (Fuji Film).

2.4. Bimolecular fluorescence complementation (BiFC) assay

To express cYFP (the C-terminal half of yellow fluorescent protein)-fused NPH3.1, pBluescript II SK⁻ NPH3.1 (see Supplementary Method S1) was digested by *Xba*I, and the resultant *NPH3.1* ORF fragment was inserted into the *Spe*I site of pBS-35SMCS-cYFP [6], generating pBS-35S-NPH3.1-cYFP. To express nYFP (the N-terminal half of YFP)-fused AGB1, pBS-35S-nYFP-AGB1 [6] was used. A mixture of pBS-35S-nYFP-AGB1 and pBS-35S-NPH3.1-cYFP (500 ng each) was used for particle bombardment to co-express NPH3.1-cYFP and nYFP-AGB1 in onion epidermal cells. Particle bombardment was performed as previously described, and YFP fluorescence was observed by fluorescence microscopy as previously described [22]. Images were processed using Canvas X software (ACD Systems).

2.5. RT-PCR

For RT PCR, plants were grown for four weeks and sampled. Total RNA was prepared using RNeasy Plant Mini Kit (Qiagen), and cDNA was synthesized from 900 ng total RNA using High Capacity RNA-to-cDNA Kit (Applied Biosystems). The cDNA was diluted 15 times by distilled water and used as template for RT-PCR. The expression of *NPH3* was examined by semi-quantitative RT-PCR, and the expression of *AGB1* was examined by quantitative real-time RT-PCR. The real-time PCR was performed using SYBR Premix EX Taq II (Perfect Real Time) (Takara) and the StepOne Real-Time PCR Systems (Applied Biosystems). Primers used for RT-PCR are shown in Supplementary Table S2.

3. Results and discussion

3.1. AGB1 interacts with NPH3

We and another group independently performed yeast two-hybrid (Y2H) screens using AGB1 as bait, and both identified NPH3 as a potential AGB1 interactor [5,6]. In our Y2H screen, *NPH3* was detected as a 5′ region-truncated form (the position 1546-2241 from the start codon) of *NPH3.1* (see Fig. 1B for the region of NPH3 used in Y2H analysis). Yeast cells could grow on the selection medium when they were co-transformed with the constructs that contain both *AGB1* and the 5′ region-truncated version of *NPH3.1* (Fig. 1A, middle panel), but not when either *AGB1* or the truncated form of *NPH3.1* was absent in the constructs (Fig. 1A, right and left panels), confirming that AGB1 and the C-terminal region of NPH3.1 interact in yeast cells. Y2H analysis using full-length NPH3.1 and AGB1 was also attempted. However, yeast transformed with pGAD full-length NPH3.1 could not grow in the control medium (data not shown).

In an *in vitro* GST pull-down assay, polyhistidine-tagged AGB1 (His-AGB1) was detected when it was reacted with GST-fused NPH3.1, NPH3.2 or BTB+I+II, a C-terminal region-truncated form of NPH3, but not when reacted with III+IV (GST-fused form), which corresponds to the central region of NPH3 (Fig. 1C and D; see Fig. 1B for diagrammatic representations of NPH3 proteins). These

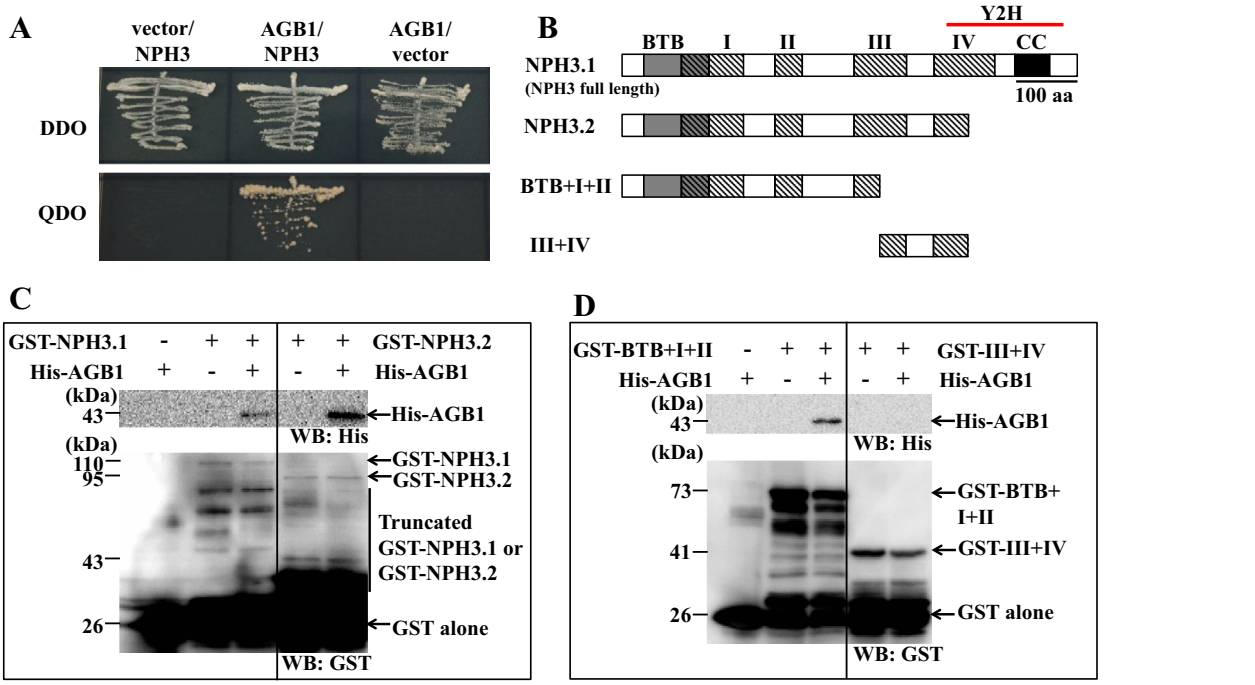

Fig. 1. Interaction between AGB1 and NPH3 in yeast and *in vitro*. (A) Yeast two-hybrid analysis of the interaction between AGB1 and NPH3. The combinations of the plasmids used for transformation of the yeast strain AH109 are indicated at the top of each panel. vector: a pGBKT7 plasmid or a pGADT7-Rec plasmid containing no insert; AGB1: pGBKT7 containing *AGB1*; NPH3: pGADT7-Rec containing a 5′ region-truncated form (the position 1546-2241) of *NPH3.1*. Transformed yeast cells were cultured on DDO (SD medium lacking tryptophan and leucine) and QDO (DDO lacking histidine and adenine) to check activation of the reporter genes *HIS3* and *ADE2*. At least 4 colonies for each genotype were tested and a representative result is shown. (B) Diagrammatic representations of NPH3 proteins. Four domains (I to IV) conserved among NPH3 homologs are shown on NPH3 by cross-hatched blocks. The BTB (broad complex, tramtrack, bric a'brac) domain and the coiled-coil (CC) domain are shown in the dark gray block and black block, respectively. The gray cross-hatched block indicates the region which the BTB domain and domain I share. The region of NPH3 used in yeast two-hybrid (Y2H) analysis is indicated by the red line. (C and D) *In vitro* GST pull-down assay between GST-fused NPH3.1 (GST-NPH3.1) or GST-fused NPH3.2 (GST-NPH3.2) and polyhistidine-tagged AGB1 (His-AGB1) (C), or GST-fused BTB+I+II, a C-terminal region-truncated form of NPH3, (GST-BTB+I+II) or GST-fused III+IV, a variant containing only the central region of NPH3, (GST-III+IV) and His-AGB1 (D). GST-NPH3.1, GST-NPH3.2, GST-BTB+I+II, GST-III+IV and His-AGB1 were expressed in *E. coli* and used for the analysis. The presence or absence of each protein in the reaction mixture is shown as + or −, respectively. His-AGB1 was analysed by Western blotting using a polyhistidine probe, HisProbe-HRP (WB: His). GST-NPH3.1, GST-NPH3.2, GST-BTB+I+II and GST-III+IV were analysed by western blotting using anti-GST antibody (WB:GST). Experiments were performed 4 times and a representative result is shown.

results suggest that the N-terminal region rather than the C-terminal region of NPH3 interacts with AGB1 *in vitro*. This is not consistent with the Y2H analysis, where the C-terminal region of NPH3.1 was responsible for the AGB1–NPH3 interaction. It might be possible that the interaction between AGB1 and the C-terminal region of NPH3.1 requires cellular components. In yeast, the N-terminal region of NPH3 might mislocalize and/or destabilize NPH3.1.

In a bimolecular fluorescence complementation (BiFC) assay using onion cells, YFP (yellow fluorescent protein) fluorescence was recovered in cell periphery when nYFP (the N-terminal region of YFP)-fused AGB1 and cYFP (the C-terminal region of YFP)-fused NPH3.1 were co-expressed (Fig. 2), suggesting that AGB1 and NPH3.1 interact in the plasma membrane in plant cells. AGB1 has been reported to be localized to the cytosol, the nucleus, the Golgi apparatus and the plasma membrane [6,9,23,24], while NPH3.1 is localized to the plasma membrane [10,13]. Thus, the localization of NPH3.1 is thought to limit the localization of the AGB1-NPH3.1 BiFC to the plasma membrane.

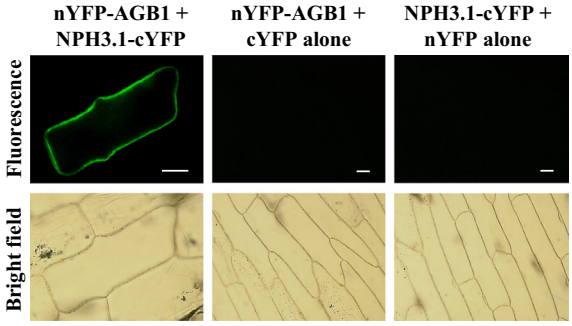

Fig. 2. Interaction between AGB1 and NPH3 *in planta*. The ORF of *AGB1* was cloned in frame behind the coding sequence of the N-terminal region of YFP (nYFP) to express nYFP-fused AGB1 (nYFP-AGB1), and the ORF of *NPH3.1* was cloned in frame in front of the coding sequence of the C-terminal region of YFP (cYFP) to express cYFP-fused NPH3.1 (NPH3.1-cYFP). These constructs were co-introduced into onion epidermal cells via particle bombardment. Combinations of co-expressed proteins are shown at the top of each panel. cYFP alone and nYFP alone were used as controls. More than 20 cells were observed and a representative cell is shown. Scale bars = 50 μm.

3.2. AGB1 is involved in phototropism

We utilized two new *nph3* mutant alleles, *nph3-7* (Salk_110039) and *nph3-8* (CS322676), for physiological analyses. They have T-DNA insertion in *NPH3* (Supplementary Fig. S1A and B), and have no detectable level of *NPH3* transcripts (Supplementary Fig. S1C). To generate *agb1/nph3* double mutants (DMs), we crossed the *nph3-7* mutant with *agb1-2* mutant [20]. Two DMs were obtained; DM#1-1-2 and DM#11-1-2 (Supplementary Fig. S2). In a previous study, *NPH3*-null mutations completely abolished the phototropic response of etiolated seedlings [10]. In agreement with this result, the phototropic response of etiolated seedlings was abolished in both *nph3-7* and *nph3-8*. Interestingly, the *AGB1*-null mutants *agb1-1* and *agb1-2* both showed weaker phototropic responses than the wild type. The phototropic response was completely abol-

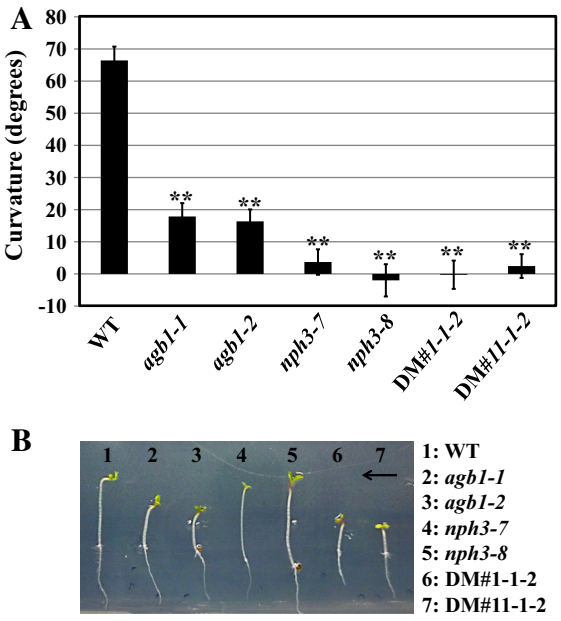

Fig. 3. AGB1 is involved in phototropism. (A) Plants of each genotype were grown in the dark for 3 days, exposed to unilateral blue light for 20 h, and photographed to measure hypocotyl curvature. WT: wild type; DM#1-1-2 and DM#11-1-2: *agb1/nph3* double mutants. Data are means ± SE of 23 seedlings. **, $p < 0.005$ vs. wild type, *t*-test. (B) A representative seedling is shown for each genotype. Arrow shows the direction of blue light.

ished in the *agb1-2/nph3-7* double mutants as in *nph3-7* and *nph3-8* (Fig. 3A and B). These results suggest that AGB1 is involved in the phototropic responses. NPH3 regulates auxin polar transport as a downstream step in phototropic responses [12,15,25], and AGB1 is involved in regulating auxin responses and/or transport [3,19,20]. Thus, AGB1 might play a role in the NPH3-dependent regulation of auxin polar transport. The expression level of *AGB1* gene was lower in the *nph3* mutants than in the wild type (Supplementary Fig. S3), raising the possibility that NPH3 positively regulates the expression of *AGB1* gene. No difference in expression of *NPH3* gene was observed between the wild type and the *agb1* mutant (Supplementary Fig. S4).

In conclusion, AGB1 physically interacts with NPH3, and is involved in the hypocotyl phototropic response. Further studies are required to elucidate how AGB1 is involved in the NPH3-mediated regulation of phototropism.

Acknowledgments

We are grateful to RIKEN BRC and ABRC for providing materials. This work was supported by a Grant-in-aid for Scientific Research (22-2144) to DT.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bbrc.2014.01.106.

References

[1] D. Urano, J.G. Chen, J.R. Botella, et al., Heterotrimeric G protein signalling in the plant kingdom, Open Biol. 3 (2013) 120186.
[2] H.X. Wang, R.R. Weerasinghe, T.D. Perdue, et al., A golgi-localized hexose transporter is involved in heterotrimeric G protein-mediated early development in Arabidopsis, Mol. Biol. Cell 17 (2006) 4257–4269.
[3] Y. Mudgil, J.F. Uhrig, J. Zhou, et al., Arabidopsis N-MYC DOWNREGULATED-LIKE1, a positive regulator of auxin transport in a G protein-mediated pathway, Plant Cell 21 (2009) 3591–3609.
[4] E.J. Friedman, H.X. Wang, K. Jiang, et al., Acireductone dioxygenase 1 (ARD1) is an effector of the heterotrimeric G protein β subunit in Arabidopsis, J. Biol. Chem. 286 (2011) 30107–30118.
[5] K. Klopffleisch, N. Phan, K. Augustin, et al., Arabidopsis G-protein interactome reveals connections to cell wall carbohydrates and morphogenesis, Mol. Syst. Biol. 7 (2011) 532.
[6] D. Tsugama, H. Liu, S. Liu, et al., Arabidopsis heterotrimeric G protein β subunit interacts with a plasma membrane 2C-type protein phosphatase, PP2C52, Biochim. Biophys. Acta 2012 (1823) 2254–2260.
[7] S. Kobayashi, D. Tsugama, S. Liu, et al., A U-Box E3 Ubiquitin Ligase, PUB20, interacts with the Arabidopsis G-Protein β Subunit, AGB1, PLoS One 7 (2012) e49207.
[8] D. Tsugama, S. Liu, T. Takano, A bZIP protein, VIP1, interacts with Arabidopsis heterotrimeric G protein β subunit, AGB1, Plant Physiol. Biochem. 9 (2013) 240–246.
[9] J. Kansup, D. Tsugama, S. Liu, et al., The Arabidopsis adaptor protein AP-3μ interacts with the G-protein β subunit AGB1 and is involved in abscisic acid regulation of germination and post-germination development, J. Exp. Bot. 64 (2013) 5611–5621.
[10] A. Motchoulski, E. Liscum, Arabidopsis NPH3: a NPH1 photoreceptor-interacting protein essential for phototropism, Science 286 (1999) 961–964.
[11] P. Lariguet, I. Schepens, D. Hodgson, et al., PHYTOCHROME KINASE SUBSTRATE 1 is a phototropin 1 binding protein required for phototropism, Proc. Natl. Acad. Sci. USA 103 (2006) 10134–10139.
[12] Y. Wan, J. Jasik, L. Wang, et al., The signal transducer NPH3 integrates the phototropin1 photosensor with PIN2-based polar auxin transport in Arabidopsis root phototropism, Plant Cell 24 (2012) 551–565.
[13] S. Inoue, T. Kinoshita, A. Takemiya, et al., Leaf positioning of Arabidopsis in response to blue light, Mol. Plant 1 (2008) 15–26.
[14] U.V. Pedmale, R.B. Celaya, E. Liscum, Phototropism: mechanism and outcomes, Arabidopsis Book 8 (2010) e0125.
[15] D. Roberts, U.V. Pedmale, J. Morrow, et al., Modulation of phototropic responsiveness in Arabidopsis through ubiquitination of phototropin 1 by the CUL3-Ring E3 ubiquitin ligase CRL3(NPH3), Plant Cell 23 (2011) 3627–3640.
[16] Q. Wei, W. Zhou, G. Hu, et al., Heterotrimeric G-protein is involved in phytochrome A-mediated cell death of Arabidopsis hypocotyls, Cell Res. 18 (2008) 949–960.
[17] J.F. Botto, S. Ibarra, A.M. Jones, The heterotrimeric G-protein complex modulates light sensitivity in Arabidopsis thaliana seed germination, Photochem. Photobiol. 85 (2009) 949–954.
[18] K.M. Warpeha, S.S. Lateef, Y. Lapik, et al., G-protein-coupled receptor 1, G-protein Galpha-subunit 1, and prephenate dehydratase 1 are required for blue light-induced production of phenylalanine in etiolated Arabidopsis, Plant Physiol. 140 (2006) 844–855.
[19] K.A. Lease, J. Wen, J. Li, et al., A mutant Arabidopsis heterotrimeric G-protein β subunit affects leaf, flower and fruit development, Plant Cell 13 (2001) 2631–2641.
[20] H. Ullah, J.G. Chen, B. Temple, et al., The β-subunit of the Arabidopsis G protein negatively regulates auxin-induced cell division and affects multiple developmental processes, Plant Cell 15 (2003) 393–409.
[21] T. Knauer, M. Dümmer, F. Landgraf, et al., A negative effector of blue light-induced and gravitropic bending in Arabidopsis, Plant Physiol. 156 (2011) 439–447.
[22] C.Q. Zhang, S. Nishiuchi, S. Liu, et al., Characterization of two plasma membrane protein 3 genes (*PutPMP3*) from the alkali grass, Puccinellia tenuiflora, and functional comparison of the rice homologues, *OsLti6a/b* from rice, BMB Rep. 41 (2008) 448–454.
[23] M.J. Adjobo-Hermans, J. Goedhart, T.W. Gadella Jr., Plant G protein heterotrimers require dual lipidation motifs of Galpha and Ggamma and do not dissociate upon activation, J. Cell Sci. 119 (2006) 5087–5097.
[24] D.J. Anderson, J.R. Botella, Expression analysis and subcellular localization of the Arabidopsis thaliana G-protein beta-subunit AGB1, Plant Cell Rep. 26 (2007) 1469–1480.
[25] T. Sakai, K. Haga, Molecular genetic analysis of phototropism in Arabidopsis, Plant Cell Physiol. 53 (2012) 1517–1534.