Ribosome biogenesis factor OLI2 and its interactor BRX1-2 are associated with morphogenesis and lifespan extension in *Arabidopsis thaliana*

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Abstract  Mutations that reduce the expression of ribosomal proteins (RPs) or limit the activity of ribosome biogenesis-related factors frequently cause physiological and morphological changes in *Arabidopsis*. *Arabidopsis OLI2/NOP2A*, a homolog of yeast Nop2, encodes a nucleolar methyltransferase that is required for the maturation of the 25S ribosomal RNA of the 60S large ribosomal subunit. Mutant *oli2* plants exhibit pointed leaves and shortened primary roots. In this study, detailed phenotypic analysis of *oli2* mutant and *OLI2* overexpressor lines revealed a range of phenotypes. Seeds produced by *oli2* mutant and *OLI2* overexpressor plants were lighter and heavier than wild-type seeds, respectively. Seeds of the *oli2* mutant also showed delayed germination, whereas seeds from the *OLI2* overexpressor lines germinated earlier than the wild type. The *oli2* mutant also had fewer and shorter lateral roots than the wild type. The lateral root development phenotype in the *oli2* mutant was similar to that of auxin-related mutants, but was not enhanced by exogenously supplied auxin. Furthermore, the *oli2* mutant and *OLI2* overexpressor lines were hypersensitive and less sensitive to high concentrations of sugar, respectively. Split-GFP-based bimolecular fluorescence complementation analysis revealed that OLI2 interacted with a nucleolar protein, BRX1-2, which is involved in rRNA processing for the large ribosomal subunit. Moreover, overexpression of *OLI2* and *BRX1-2* caused similar morphological changes, including extension of plant lifespans. These results suggest that the functions of OLI2 and its interactor BRX1-2 are intimately associated with a range of developmental events in *Arabidopsis*.

Key words: *Arabidopsis thaliana*, auxin, plant morphology, pre-rRNA processing-associated factor, ribosome biogenesis.

Introduction

Cytosolic ribosome in plants is a large protein-RNA complex consisting of approximately 80 ribosomal proteins (RPs) and four ribosomal RNAs (25S, 18S, 5.8S, and 5S rRNA) as scaffolds (Sáez-Vásquez and Delseny 2019; Weis et al. 2015a). Ribosome biogenesis proceeds through a number of steps, including processing and post-transcriptional modification of rRNAs and post-translational modification of RPs, which are mediated by ribosome biogenesis factors (RBFs) (Sáez-Vásquez and Delseny 2019; Weis et al. 2015a).

In *Arabidopsis*, knockdown mutations for single-copy genes encoding RPs or RBFs, or loss-of function mutations for one of the paralogous genes encoding RPs or RBFs, very frequently cause morphological abnormalities and physiological and developmental defects, including inhibition of embryogenesis, development of pointed true leaves with abnormal vascular pattern, shorter primary roots, and altered responses to cold temperature, sugar, and antibiotics (Reviewed in Weis et al. 2015a). Because these phenotypes resemble the phenotypes of auxin-related mutants, some ribosome-related mutants are thought to exhibit their phenotypes through defects in auxin signaling or biogenesis. Indeed, alongside the typical phenotypes of ribosome-related mutants (e.g., short primary roots, abnormal leaf morphology with altered vascular structure, and defects in lateral root development), auxin distribution, response, and transport were affected in a mutant of *LSG1*, which encodes a circularly permuted GTPase involved in ribosome biogenesis (Weis et al. 2014; Zhao et al. 2015). Furthermore, recent studies revealed that the ribosomal stress response, also termed the nucleolar stress response and defined as a stress resulting from defects in ribosome biogenesis, was associated with morphological abnormalities in some ribosome-related

Abbreviations: RP, ribosomal protein; rRNA, ribosomal RNA; RBF, ribosome biogenesis factor.

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mutants (Maekawa et al. 2018a; Ohbayashi and Sugiyama 2018; Ohbayashi et al. 2017; Wang et al. 2020). For example, the knockdown mutation of *ARABIDOPSIS PUMILIO PROTEIN24* (APUM24), which encodes a protein involved in the removal of internal transcribed spacer 2 (ITS2) from pre-rRNA and in the production of 25S ribosomal RNA for the large (60S) ribosomal subunit, resulted in changes in nucleolar size and morphological abnormalities dependent on high concentrations of sugar in the growth medium (Maekawa and Yanagisawa 2018b; Maekawa et al. 2018a). Furthermore, Arabidopsis SRIW1/ANAC082 was shown to function as a key transcription factor for the ribosomal stress response, leading to leaf morphological abnormalities and inhibition of root elongation (Ohbayashi et al. 2017).

An Arabidopsis RBF, OLIGOCELLULA2 (OLI2)/NOP2A (hereinafter called OLI2), is a homolog of yeast methyltransferase Nop2, which methylates the cytosine residue at position 2870 of 25S rRNA (Fujikura et al. 2009; Sharma et al. 2013). In yeast, depletion of Nop2 results in increased accumulation of immature 27S rRNA and corresponding decreases in levels of mature 25S and 5.8S rRNAs (Hong et al. 1997). Mutation of neither OLI2 nor NOP2B, a paralog of OLI2, affected the methylation level of the cytosine at position 2860 of Arabidopsis 25S rRNA, equivalent to the cytosine residue at position 2870 of yeast 25S rRNA (Burgess et al. 2015). The *oli2* *nop2b* double mutant was likely lethal, and thereby OLI2 and NOP2B were proposed to have redundant roles in the methylation of 25S rRNA that were essential for growth in Arabidopsis (Burgess et al. 2015). However, the *nop2b* mutant did not show any apparent phenotype (Burgess et al. 2015), whereas the *oli2* mutant showed decreased numbers of cells in the first true leaves and also exhibited rRNA processing defects (Fujikura et al. 2009; Kojima et al. 2018). Thus, it is likely that OLI2, rather than NOP2B, plays the major role in ribosome biogenesis.

In this study, the *oli2* mutant and OLI2 overexpressor lines were analyzed to investigate the effects of loss or enhancement of OLI2 activity on growth and development. Previous research showed that OLI2 and BRX1-2, which is involved in pre-rRNA processing and is required for biogenesis of the large ribosomal subunit, co-immunoprecipitated with APUM24 (Maekawa et al. 2018a). The physical interactions between OLI2 and BRX1-2 were therefore also assessed in this study. Phenotypic analysis of newly generated *BRX1-2* overexpressor and *oli2 brx1-2* double mutant lines revealed that OLI2 and BRX1-2 overexpressors exhibited similar phenotypes. These results indicate that OLI2 and its interactor BRX1-2 are involved in diverse aspects of growth in Arabidopsis.

### Materials and methods

#### Plant materials and growth conditions

*Arabidopsis thaliana* ecotype Columbia (Col-0) was used as the wild type, and all T-DNA insertion lines and mutants used in this study were in the Col-0 background. Seeds of two T-DNA insertion lines, SALK_129648 for *oli2* (Fujikura et al. 2009) and GABI_771C02 (Weis et al. 2015b) for *brx1-2*, were provided by the Arabidopsis Biological Resource Center (Alonso et al. 2003) and GABI-Kat (Rosso et al. 2003), respectively. The *oli2* *2* knockout mutant (Fujikura et al. 2009) was used as the *oli2* mutant in this study. Seeds were sterilized and sown on agar plates containing half-strength Murashige and Skoog medium (1/2 MS) supplemented with 1% sucrose. After a 2-day cold treatment, the plates were placed at 23°C under diurnal light conditions with a day/night cycle of 16/8 h and approximately 70 µmol m$^{-2}$ s$^{-1}$ light. After 2 weeks, seedlings on plates were transferred onto peat containing nutrients (Sakatanotane Co., Yokohama, Japan) and further grown at 23°C under continuous

### Table 1. List of primer sequences.

<table>
<thead>
<tr>
<th>Primer name</th>
<th>Sequence (5'–3')</th>
</tr>
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<tbody>
<tr>
<td>Vector construction</td>
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<tr>
<td>OLI2-5' entry</td>
<td>CACCATGCTGCCCTCACTCTGTAAC</td>
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<tr>
<td>OLI2-3' entry</td>
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<tr>
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<td>OLI2-R</td>
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<tr>
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</tr>
<tr>
<td>UBQ10-0-F</td>
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</tr>
<tr>
<td>UBQ10-R</td>
<td>CGACTTGTACATTGAAAAAGAGAAGATACAGG</td>
</tr>
</tbody>
</table>

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and incubated for 2 h. Plates were transferred onto 30 µM IAA-containing agar plates to study its effects on gene expression, seedlings grown on control agar plates (1/2 MS, 1% sucrose, and 0.8% agar) and grown for 4 days. Seedlings were then transferred to agar plates containing various concentrations of IAA and grown for a further 3 days. Measurements of the total length of lateral roots and the number of emerged lateral roots of the seedlings were performed under a stereoscopic microscope. To investigate IAA effects on gene expression, seedlings grown on control agar plates were transferred onto 30 µM IAA-containing agar plates and incubated for 2 h.

**Measurement of anthocyanin contents**

Anthocyanin contents were determined as described in Mehrten et al. (2005) with minor modifications. In brief, approximately 10 mg of whole plant tissue was submerged in 600 µl of acidic methanol (1% HCl, w/v) and incubated overnight at 4°C with gentle shaking. Anthocyanin was extracted with 400 µl distilled water and 400 µl chloroform. Absorption of the extracts was measured at 530 nm and 657 nm. Relative anthocyanin contents were calculated using the formula A530–(A675×0.25).

**Results and discussion**

**Seed and seedling phenotypes of the oli2 mutant and OLI2 overexpressors**

Experiments were devised to investigate the effects of loss or enhancement of OLI2 activity on growth and development. Two independent transgenic lines (#1 and #2) that expressed OLI2-GFP under the control of the 35S promoter were generated. Total OLI2 transcripts from the endogenous OLI2 gene and the introduced OLI2-GFP gene in the two independent lines were higher than native OLI2 transcript levels in the wild type (Figure 1A), and the transgenic lines were therefore designated as OLI2 overexpressors. The oli2-2 knockout mutant (Fujikura et al. 2009) was used as the oli2 mutant in this study.

Arabidopsis RP and RBF mutants frequently exhibit delayed embryogenesis and germination as well as the formation of leaves with abnormal shapes, such as pointed and/or serrated leaves (reviewed in Weis et al. 2015a), and the oli2 mutant was also reported to exhibit pointed leaves (Fujikura et al. 2009). Seed development and seedling growth was therefore examined in the oli2 mutant and the OLI2 overexpressors. The mass of 200 seeds was compared, and seeds from the oli2 mutant and OLI2 overexpressors were lighter and heavier, respectively, than seeds from the wild type (Figure 1B, C). Analysis of germination rates after imbibition indicated that seed germination was delayed in the oli2 mutant, whereas seeds from OLI2 overexpressors germinated earlier (Figure 1D). The pointed and serrated true leaves (Figure 1E) and short primary root (Figure 1F) phenotypes that were reported previously in the oli2 mutant (Fujikura et al. 2009) were confirmed. Overexpression of OLI2 had no apparent effects on leaf development (Figure 1E) but produced longer primary roots (Figure 1F). These results indicated that
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the levels of expression of OLI2 had effects on growth and development that were more broad ranging than previously reported.

**IAA responses in the oli2 mutant and OLI2 overexpressors**

The oli2 mutant and OLI2 overexpressors exhibited root and leaf development phenotypes, which might be associated with auxin signaling (Horiguchi et al. 2012; Huang et al. 2016). In fact, Zhou et al. (2010) reported that auxin regulates root elongation through induction of the expression of tyrosylprotein sulfotransferase gene involved in sulfation of root meristem growth factors (RGFs), a critical step in activation of RGFs. Thus, we hypothesized that auxin signaling modifications might be responsible for the root phenotypes observed in the oli2 mutant and the OLI2 overexpressors. To test this possibility, seedlings grown for 4 days in the absence of IAA were grown in the presence of different concentrations of IAA (0–30 nM), and positive effects were seen on lateral root development (in terms of number and total length) (Figure 2A, B). Primary root length in the oli2 mutant was shorter than in the wild type, independent of IAA, but the negative effect of IAA on primary root length remained apparent in the oli2 mutant (Figure 2A, B). Similar negative effects were also observed in the OLI2 overexpressor lines. Furthermore, positive effects on lateral root development were observed in the oli2 mutant and the OLI2 overexpressors, although the effect of IAA in the oli2 mutant was mitigated due to strong inhibition of lateral root development (Figure 2A, B).

Next, expression levels of auxin-inducible genes IAA5, IAA19, and PIN7 (Lewis et al. 2011; Nakamura et al. 2003) were examined in the wild type, the oli2 mutant, and the OLI2 overexpressors (Figure 2C). Expression of PIN7 in the oli2 mutant was slightly higher than in the wild type, independent of IAA treatment, but expression levels of IAA5 and IAA19 were mostly comparable in the wild type, the oli2 mutant, and the OLI2 overexpressors. These results suggested that auxin sensitivity in the oli2 mutant and OLI2 overexpressors was comparable with that of the wild type.

**AUXIN RESPONSE FACTORS (ARFs)** are transcriptional activators that play a central role in the auxin response, and ARF protein levels are translationally regulated via upstream open reading frames (uORFs) in the 5′-transcript leader sequences of ARF mRNAs. Therefore, the ribosome function may affect auxin responses through uORF-mediated translational regulation of ARFs (Nishimura et al. 2005; Rosado et al. 2012). Indeed, Arabidopsis ribosomal protein mutants, including stv1/rpl24, rpl4d, and rpl5a, showed phenotypes similar to those of auxin-related mutants (Nishimura et al. 2005; Rosado et al. 2012). Although we did not find any significant effect of exogenously supplied auxin on the phenotype of the oli2 mutant and OLI2 overexpressors or expression levels of auxin-
inducible genes in these plants (Figure 2), it remains possible that the growth and developmental phenotypes in the oli2 mutant and the OLI2 overexpressors are due to alterations in processes involved in auxin biosynthesis, transport, signaling, or response. This possibility needs to be carefully considered by further analysis.

Sugar response of the oli2 mutant and OLI2 overexpressors

Transcription of ribosomal DNA and genes encoding RPs and proteins involved in ribosome biogenesis is generally activated by sugar supplementation in plants (Ishida et al. 2016; Maekawa and Yanagisawa 2018b; Maekawa et al. 2018a). Thus, the effect of sugar supplementation on OLI2 expression was examined next. Supplementation with various metabolizable sugars (fructose, glucose, and sucrose) significantly induced OLI2 expression, whereas treatment with non-metabolizable sugar (mannitol), which served as an osmotic control, did not (Figure 3A). Based on the finding that expression of OLI2 was sugar-inducible, growth of the oli2 mutant and OLI2 overexpressors was examined on agar plates containing 0, 50, or 250 mM glucose, 50 mM mannitol, or 50 mM glucose with 200 mM mannitol (Figure 3B, C). High concentrations of metabolizable sugar repress plant growth and promote the accumulation of anthocyanin, a sugar stress marker, in Arabidopsis seedlings (Martin et al. 2002). These effects were much more evident in the oli2 mutant than in the wild type, whereas the OLI2 overexpressor lines were more tolerant to high concentrations of metabolizable sugar (250 mM glucose). These effects were not observed with mannitol treatment, eliminating the possibility that these results were due to osmotic stress (Figure 3B, C). Thus, like other ribosome biogenesis-associated mutants, including apum24 (Maekawa et al. 2018a), rh57 (Hsu et al. 2014), and mdn1 (Li et al. 2019), oli2 is hypersensitive to sugar, confirming an intimate relationship between energy source (sugar) and ribosome biosynthesis.

OLI2 interacts with BRX1-2

BRX1-2 is a nucleolar protein that plays an important role in pre-rRNA processing, and its mutant shows pleiotropic phenotypes such as serrated leaves, germination delay, root growth defects, sugar hypersensitivity, and rRNA processing defects (Maekawa et al. 2018a; Weis et al. 2015b). The phenotype of the brix1-2 mutant closely resembles that of the oli2 mutant. Furthermore, our previous research found that BRX1-2 and OLI2 co-immunoprecipitated with APUM24.
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Thus, we tested the physical interaction between OLI2 with BRX1-2 using BiFC analysis with BRX1-2 fused to nGFP (BRX1-2-nGFP) and OLI2 fused to cGFP (OLI2-cGFP). When these proteins were transiently co-expressed in *Nicotiana benthamiana* leaves, GFP fluorescence was observed that perfectly overlapped with red fluorescence from mCherry fused to fibrillarin1 (FIB1), a nucleolus-localized marker protein (Barneche et al. 2000) (Figure 4A). No GFP fluorescence was detected in cells expressing BRX1-2-nGFP or OLI2-cGFP alone, confirming that OLI2 physically interacted with BRX1-2 in the nucleolus.

Next, we generated an *oli2 brx1-2* double mutant to investigate the genetic interaction between OLI2 and BRX1-2. Some *oli2 brx1-2* seedlings had a monocotyledon or tricotyledon, but this phenomenon was not observed in *oli2* or *brx1-2* single mutant seedlings (Figure 4B, Table 2), suggesting that *oli2* mutation in combination with the *brx1-2* mutation affects cotyledon development. The number of cotyledons is also known to be highly associated with auxin-regulated processes. Indeed, the mutants of the *YUCCA* family, *TIR* family, and *MONOPTEROS/ARF5*, which are involved in auxin biosynthesis, reception, and signaling, respectively, develop monocotyledon (reviewed in Chandler 2008). The mutants for *PIN1* auxin transporters and a mutant of *PINOID*, which encodes the serine/threonine kinase that catalyzes phosphorylation of *PIN1*, also show various cotyledon phenotypes, including monocotyledon and tricotyledon (Bennett et al. 1995; Huang et al. 2010). Development of a monocotyledon or tricotyledon was also reported in mutants of ribosome biogenesis factors, such as an Arabidopsis mutant with mutations on both OLI2 and GDP1 encoding a G-patch domain-containing RBF (Kojima et al. 2018). In addition, single mutants for ribosome biogenesis genes *LSG1-2*, which encodes a
GTPase, and MTR4, which encodes a putative RNA helicase, developed altered numbers of cotyledons (Lange et al. 2011; Weis et al. 2014). Thus, the development of monocotyledon and tricotyledons in the oli2 brx1-2 double mutant again suggests the intimate relationship between ribosome biogenesis and auxin response.

OLI2 and BRX1-2 are involved in pre-rRNA processing; however, 35S, 27SA, 27SB, P-A3, and 18S-A3 pre-rRNAs over-accumulated in the oli2 mutant (Kojima et al. 2018), while 33S, 32S, 27SA2, and 20S pre-rRNAs over-accumulated and reduced P-A3 in the brx1-2 mutant (Weis et al. 2015b). Therefore, the accumulation pattern of pre-rRNAs in the oli2 brx1-2 double mutant is expected to be different from those in the oli2 and brx1-2 single mutants. Comparison of pre-rRNA accumulation patterns in these mutants might provide an opportunity to investigate why the mutations for ribosome biogenesis factors affect cotyledon development.

OLI2 and BRX1-2 overexpressors show similar aberrant stem and leaf morphology characteristics

To compare the effects of overexpression of OLI2 and BRX1-2, two independent transgenic Arabidopsis lines were generated expressing BRX1-2-GFP under the control of the 35S promoter. Total BRX1-2 transcript levels from the endogenous BRX1-2 gene and the introduced BRX1-2-GFP gene in the two independent lines were higher than native BRX1-2 transcript levels in the wild type (Figure 5A). The phenotype of these BRX1-2 overexpressor lines was compared with that of the OLI2 overexpressor lines. Five-week-old OLI2 and BRX1-2 overexpressors showed similar drastic morphological changes, including very short stems (Figure 5B–D) and twisted leaves (Figure 5C–E). The oli2 and brx1-2 single mutants did not show severe morphological changes at this growth stage (Figure 5B, C). Since short stem and curled leaves have also been reported in auxin-related mutants, such as the gain-of-function mutants of IAA3, 8, and 28 (Rogg et al. 2001; Tian and Reed 1999, Wang et al. 2013), it may be possible
to speculate that short stems and twisted leaves in the OLII and BRX1-2 overexpressors are caused by altered auxin response.

By nine weeks after germination, wild-type plants were completely withered, whereas OLII and BRX1-2 overexpressor plants had very short stems and green leaves (Figure 5F). The green leaves of the nine-week-old OLII and BRX1-2 overexpressor plants may indicate a long lifespan in the overexpressor lines. Our previous research showed that overexpression of two Arabidopsis RBFs, ARPF2 and ARRS1, which are probably involved in maturation of the ribosome large subunit, also produced short height and long lifespan phenotypes (Maekawa et al. 2018c). No such phenotypes were observed in transgenic plants overexpressing PRH75, which encodes a DEAD-box RNA helicase involved in pre-rRNA processing, or APUM24 (Maekawa et al. 2018c). Thus, overexpression of RBFs does not always cause shorter stems and long lifespan. Further clarification of which RBF features cause these phenotypes upon overexpression and characterization of ribosome biosynthesis in these overexpressors would assist our understanding of how distinct abnormalities in ribosome biosynthesis lead to different phenotypes in plants.

Conclusion
In this study, we showed that a loss-of-function mutant for OLII, which encodes a putative methyltransferase involved in ribosome biogenesis, exhibited abnormalities in a variety of developmental processes including germination, root and leaf development, and sugar response, although sensitivity to auxin was maintained in the mutant. In addition, another RBF, BRX1-2, was found to interact with OLII, and the oli2 brx1-2 double mutant plants develop mono- and tricotyledons, and OLII and BRX1-2 overexpressor lines exhibited similar morphological abnormalities. Because the phenotypes of these mutants and overexpressors are very similar to those of auxin-related mutants, these findings may provide new clues to reveal the relationship between ribosome biosynthesis and auxin-regulated morphogenesis in plants. Furthermore, mutants of different RBF genes showed some common and some distinct phenotypes. Therefore, studies to elucidate the reasons for these phenotypic differences of RBF mutants and to investigate abnormalities of auxin signaling and responses in ribosome-related mutants would be useful in understanding plant development.

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