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SHORT COMMUNICATION

Identification of OsMYC2-regulated senescence-associated genes in rice

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Abstract

Main conclusion **The jasmonic acid (JA)-responsive transcription factor OsMYC2 acts as a positive regulator of leaf senescence by direct regulation of some senescence-associated genes in rice.**

OsMYC2, a transcription factor (TF), acts as a positive regulator of jasmonic acid (JA) signaling involved in development and defense in rice. Here, we report that OsMYC2 plays an important role in leaf senescence under dark-induced senescence (DIS) conditions. Overexpression of *OsMYC2* significantly promoted leaf senescence, indicated by reduction of chlorophyll content under DIS conditions in rice. Leaf senescence under the DIS conditions was negatively regulated by OsJAZ8, a rice jasmonate ZIM-domain protein involved in the JA signaling pathway. OsMYC2 upregulated the expression of some senescence-associated genes (SAGs) and selectively bound to the G-box/G-box-like motifs in the promoters of some *SAG*s in vivo. These results suggest that OsMYC2 acts as a positive regulator of leaf senescence by direct- or indirect-regulation of *SAG*s in rice.

Keywords Jasmonic acid · Leaf senescence · OsMYC2 · Rice · Transcription factor · Senescence-associated gene

Abbreviations

DIS	Dark-induced senescence
JA	Jasmonic acid
JAZ	Jasmonate ZIM domain
PR	Pathogenesis-related
SAG	Senescence-associated gene
TF	Transcription factor
Xoo	*Xanthomonas oryzae* pv. *oryzae*

Introduction

The plant hormone jasmonic acid (JA) and its derivatives, such as amino acid conjugates of JA, are plant-signaling compounds involved in the regulation of defense and development in plants, including rice. Rice is one of the most important crops worldwide and a model for molecular studies on other monocotyledonous species (Turner et al. 2002; Avanci et al. 2010; Kanno et al. 2012; Tamaoki et al. 2013). Treatment with JA upregulates many pathogenesis-related (PR) genes (Mei et al. 2006; Yamada et al. 2012), increases the production of phytoalexins, sakuranetin, and momilactone A (Nojiri et al. 1996; Tamogami et al. 1997; Riemann et al. 2013; Ogawa et al. 2017) and the accumulation of plant volatile compounds in rice (Tanaka et al. 2014; Taniguchi et al. 2014a, b; Yoshitomi et al. 2016).

Additionally, recent studies have revealed that JA modulates leaf senescence by regulating expression of some senescence-associated genes (SAGs) in *Arabidopsis* (He et al. 2002; Shan et al. 2011; Qi et al. 2015). In rice, *Oryza sativa* CORONATINE INSENSITIVE 1b (OsCOI1b), which acts as a JA receptor, promotes leaf senescence by regulating the expressions of *SAG*s under dark-induced senescence (DIS) conditions (Lee et al. 2015). Overexpression of an NAC transcription factor

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(TF), OsNAP, causes accelerated leaf senescence owing to increased accumulation of JA (Zhou et al. 2013). These findings indicate that JA plays an important role in leaf senescence of rice. However, only few studies elucidate the mechanism of JA-mediated leaf senescence at the molecular level in rice.

Recently, we found that a TF, OsMYC2, positively regulates JA signaling and plays an important role in resistance against rice bacterial blight, which is one of the most serious diseases in rice, caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) (Uji et al. 2016). Cai et al. (2014) first identified OsMYC2 as the rice homologue of AtMYC2, which is the first JAZ-interacting TF that reported and characterized as a positive regulator of the JA-mediated root-growth inhibition and a negative regulator of the JA-mediated resistance to necrotrophic pathogen in Arabidopsis (Lorenzo et al. 2004; Chini et al. 2007). OsMYC2 regulates spikelet development at reproductive stage (Cai et al. 2014) and biosynthesis of sakuranetin, a flavonoid anti-fungal phytoalexin, in rice (Ogawa et al. 2017).

Overexpression of *OsMYC2* causes rapid degradation of chlorophyll after JA treatment in rice (Uji et al. 2016). In Arabidopsis, AtMYC2 positively regulates JA-mediated leaf senescence under DIS conditions (Yu et al. 2016). These results suggest that OsMYC2 is positively involved in JA-mediated leaf senescence under DIS conditions. However, there is no available evidence on its role in JA-mediated leaf senescence in rice. Therefore, in the present study, we aimed to investigate the role of OsMYC2 in JA-mediated leaf senescence and identify OsMYC2-regulated SAGs under DIS conditions in rice.

Materials and methods

Plant materials

Rice seeds (*Oryza sativa* L. cv. Nipponbare) were kindly provided by Dr. I. Mitsuhara, National Institute of Agrobiological Sciences. Rice plants were grown from seeds under glasshouse conditions (25 ± 1 °C, 60–80% relative humidity). *OsMYC2*-overexpressing (line 14 and line 36) and *OsJAZ8ΔC*-overexpressing (line 14 and line 17) transgenic rice plants used in this study were previously developed by Uji et al. (2016) and Yamada et al. (2012), respectively. For DIS, detached leaf blades from 3-week old wild-type (WT), *OsMYC2*-overexpressing, *OsJAZ8ΔC*-overexpressing transgenic rice plants were incubated on the 3 mM Mes buffer (pH 5.8) and kept at 25 °C in complete darkness, with the abaxial side upwards, as described by Lee et al. (2015).

Chlorophyll content measurement

Leaf blades treated under DIS conditions for 2 or 4 days, respectively, were homogenized in 1 mL of 80% acetone, followed by centrifugation at 3000*g* for 10 min. Chlorophyll content was determined by the method of Arnon (1949).

qRT-PCR

Total RNA was extracted from rice leaf blades using Trizol (Thermo Fisher Scientific, Waltham, MA, USA) according to the manufacturer's instructions. qRT-PCR was performed using SYBR Premix Ex *Taq* Mixture (Takara, Shiga, Japan) in a Thermal Cycler Dice TP800 System (Takara) according to the manufacturer's instructions. The obtained data were analyzed as described by Gomi et al. (2010). Each treatment was repeated at least three times, and four leaf blades were used per replicate. The transcript levels of each gene were normalized to those of *actin* (AK060893) and compared with those of the WT to calculate the fold change in expression levels. The sequences of the gene-specific primers used in qRT-PCR are presented in Supplementary Table S1.

Chromatin immunoprecipitation (ChIP) analysis

ChIP analysis was performed using the EpiQuick Plant ChIP kit (Epigenek, Farmingdale, NY, USA) with the OsMYC2 antibody. The specificity of anti-OsMYC2 antibody has been previously confirmed by Uji et al. (2016). One gram (fresh weight) of 1-week-old *OsMYC2*-overexpressing rice seedlings (line 14) was fixed with 20 mL of 1.0% formaldehyde solution by vacuuming for 10 min. The chromatin DNA was extracted and sheared to 200- to 1000-bp fragments by sonication. A total of 100 µL of the sheared DNA was immunoprecipitated with 1 µg of anti-OsMYC2 antibody at 100 rpm for 90 min at room temperature. As a negative control, 1 µg of normal rabbit IgG (MBL, Nagoya, Japan) was used. DNA fragments were released, purified, and used as templates for qPCR using specific primers, sequence of which are presented in Supplementary Table S2. qPCR was performed using SYBR Premix Ex *Taq* Mixture (Takara) in a Thermal Cycler Dice TP800 System (Takara) according to the manufacturer's instructions.

Results and discussion

Under DIS conditions, *OsMYC2*-overexpressing rice plants showed an accelerated leaf senescence phenotype after 2 days, whereas the leaf blades of WT were still green

(Fig. 1a). Accordingly, significantly lower total chlorophyll content was observed in *OsMYC2*-overexpressing rice plants than in the WT (Fig. 1b). We recently found that OsJAZ8 acts as a repressor of JA signaling, and transgenic rice plants overexpressing the Jas domain-truncated OsJAZ8 protein show a JA-insensitive phenotype (Yamada et al. 2012). In these transgenic rice plants, the detached leaf blades had higher chlorophyll content than that in the WT, after 4 days under DIS conditions (Fig. 1c, d). It is known that OsJAZ8 interacts with OsMYC2 in yeast cells

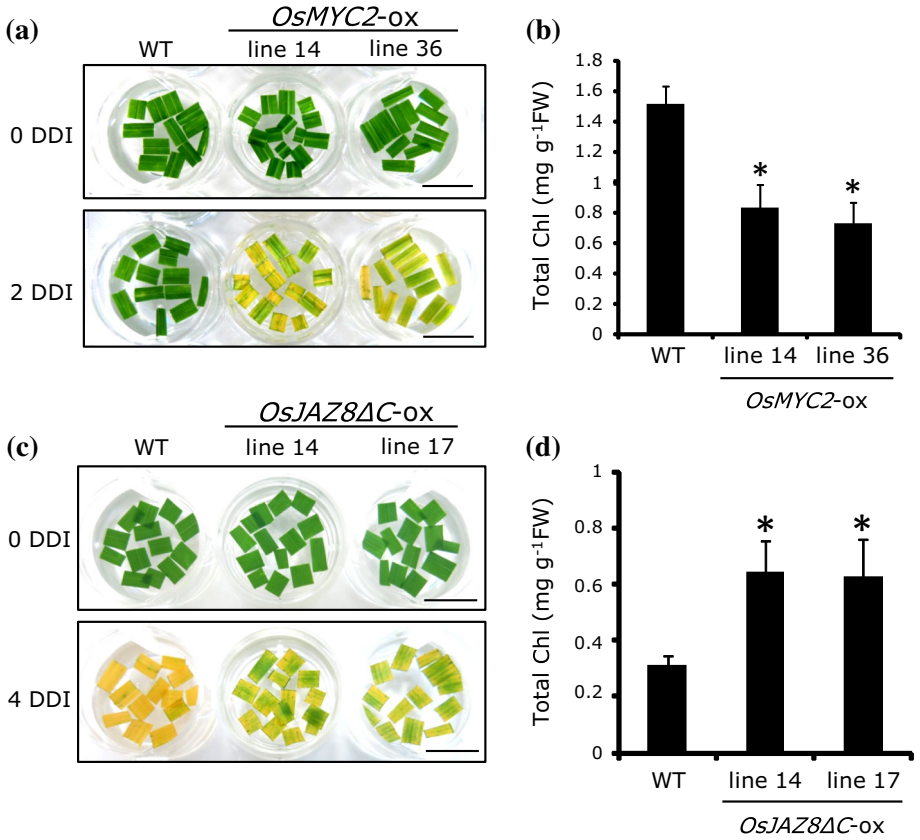

Fig. 1 Phenotypes of JA-hypersensitive or JA-insensitive transgenic rice plants under DIS conditions. **a** Photographs of leaf blades after incubation for 2 days under DIS conditions in WT and *OsMYC2*-overexpressing rice plants. *Scale bars* 10 mm. **b** Total chlorophyll contents in leaf blades after incubation for 2 days under DIS conditions in WT and *OsMYC2*-overexpressing rice plants. **c** Photographs of leaf blades after incubation for 4 days under DIS conditions in WT and *OsJAZ8ΔC*-overexpressing rice plants. *Scale bars* 10 mm. **d** Total chlorophyll contents in leaf blades after incubation for 4 days under DIS conditions in WT and *OsJAZ8ΔC*-overexpressing rice plants. **b**, **d** Data are expressed as mean ± SE of four replicates. *Asterisks* represent statistically significant difference from the WT at $P < 0.05$ (Student's *t* test)

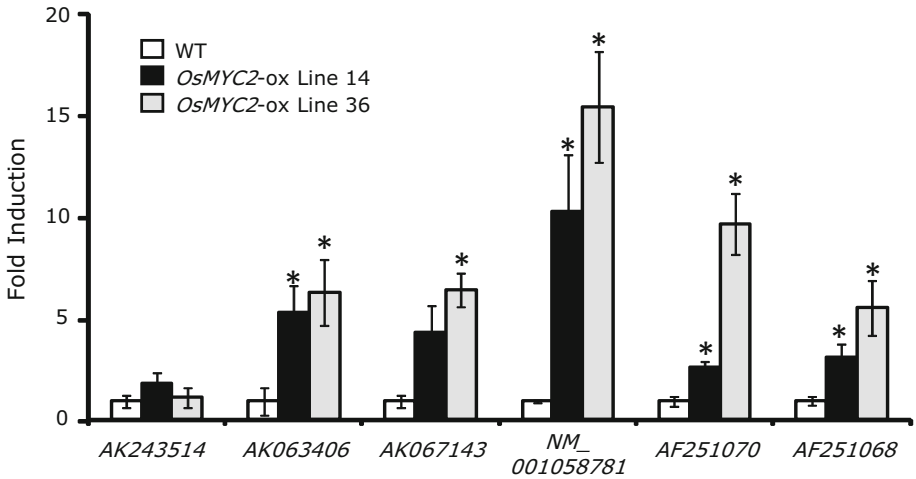

Fig. 2 Identification of OsMYC2-responsive *SAG*s. Expression levels of *SAG*s [*OsNAP* (AK243514), *OsNAP-like protein* (AK063406), *similar to SAG* (AK067143), *OsSAG12* (NM_001058781), *alanine:glyoxylate aminotransferase-like protein* (AF251070) and *raffinose synthase family protein* (AF251068)] in wild-type (WT) and *OsMYC2*-overexpressing rice plants. Data are expressed as mean ± SE of four replicates. *Asterisks* represent statistically significant difference from the WT at $P < 0.05$ (Student's *t* test)

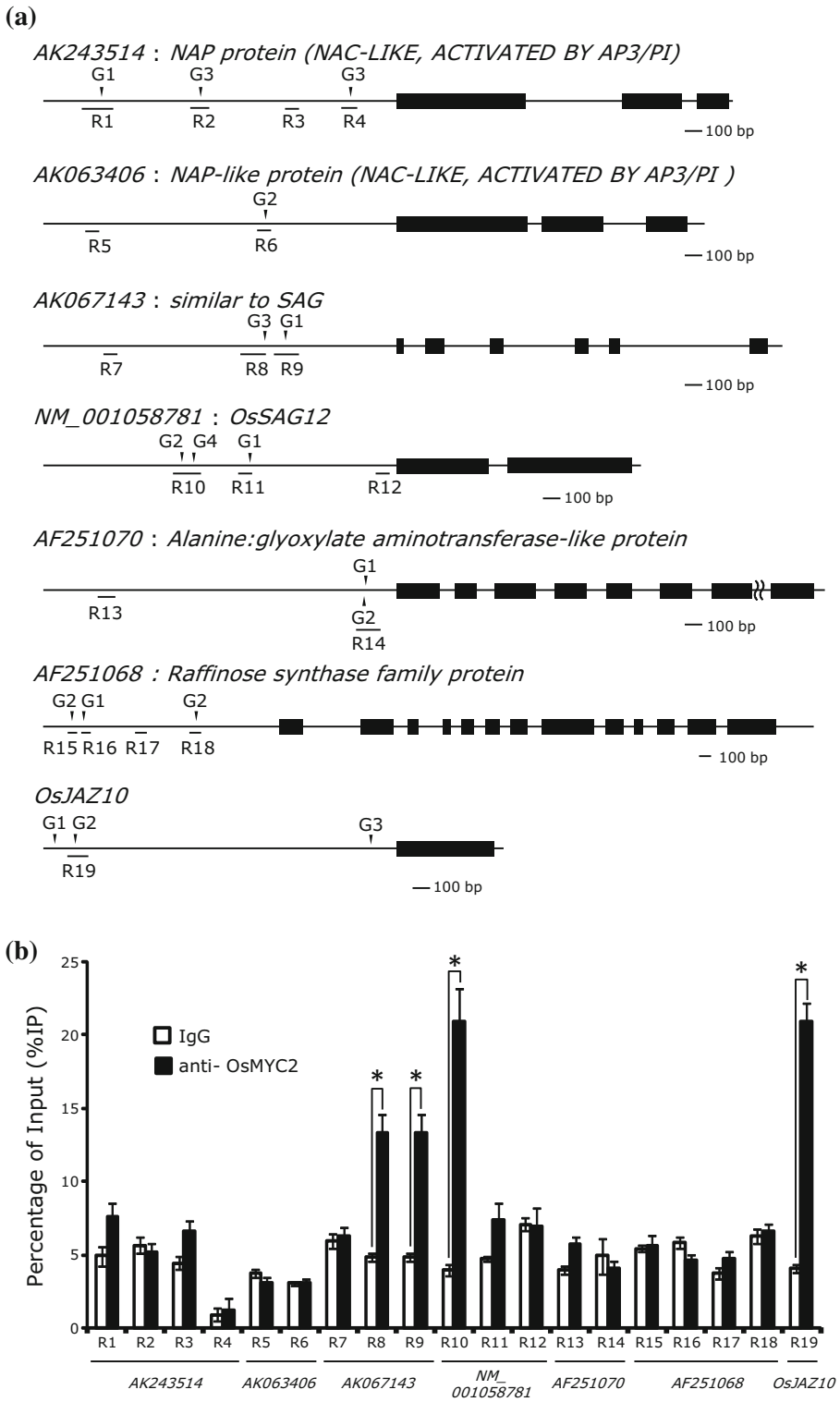

Fig. 3 OsMYC2 directly regulates some *SAG*s. **a** Diagram of the OsMYC2-responsive *SAG*s and *OsJAZ10* promoters showing the G-box/G-box-like motifs (G1, 5′-CATGTG-3′; G2, 5′-CATATG-3′; G3, 5′-CACGTG-3′; and G4, 5′-CACATG-3′). Regions amplified by qPCR after ChIP analyses are represented by R1-R19. **b** qPCR results after ChIP analysis using anti-OsMYC2 antibody. R1–R19 is the same as those in **a**. Normal IgG was used as a control. Values are the mean ± SE of four replicates. *Asterisks* represent statistically significant difference from the normal IgG at $P < 0.05$ (Student's *t* test). The experiments, performed twice, independently showed almost the same results in all cases

and negatively affects the expression of *OsMYC2* after JA treatment in rice (Uji et al. 2016), suggesting that OsJAZ8 acts as a negative regulator of OsMYC2 under DIS conditions. These results suggest that the OsMYC2-mediated JA signaling pathway is positively involved in leaf senescence under DIS conditions, and that OsMYC2-regulated SAGs exist in rice. We therefore investigated the expression levels of some known *SAG*s, which were *OsNAP* (AK243514; Zhou et al. 2013), *OsSAG12* (NM_001058781; Lee et al. 2015), *alanine:glyoxylate*

aminotransferase-like protein (AF251070; Lee et al. 2001), and *raffinose synthase family protein* (AF251068; Lee et al. 2001), in *OsMYC2*-overexpressing rice plants. In addition to these *SAG*s, we investigated the expression levels of *OsNAP-like protein* (AK063406) and *similar to SAG* (AK067143), which were identified in our previous microarray analysis using *OsMYC2*-overexpressing rice plant (Uji et al. 2016). All genes, except for *OsNAP*, were upregulated in *OsMYC2*-overexpressing rice plants under normal growth conditions in the absence of any treatment (Fig. 2), suggesting that OsMYC2 regulates expression of some *SAG*s in rice. OsNAP has been identified as a rice NAC-type TF involved in the leaf senescence (Zhou et al. 2013; Liang et al. 2014). In addition, it has been demonstrated that expression of *OsNAP* is upregulated by methyl jasmonate, and *OsNAP*-overexpression in rice causes accumulation of JA by upregulating JA-biosynthesis genes (Zhou et al. 2013). These findings suggest that OsNAP acts as a positive regulator of JA-mediated leaf senescence in rice. However, expression of *OsNAP* was not upregulated in *OsMYC2*-overexpressing rice plants, suggesting that OsMYC2 does not regulate the expression of *OsNAP*, and that unknown TF(s) regulate the expression of *OsNAP* in rice. Identification of the OsNAP-regulating TF(s) is necessary to elucidate the mechanism underlying OsNAP-mediated leaf senescence in rice.

Instead of *OsNAP*, expression of the *OsNAP-like protein* was significantly upregulated in *OsMYC2*-overexpressing rice plants (Fig. 2). OsNAP-like protein is a rice homolog of OsNAP that falls into the same cluster as that of AtNAP (Zhou et al. 2013). AtNAP acts as a positive regulator of leaf senescence in *Arabidopsis* (Guo and Gan 2006). These results suggest that the induced leaf senescence in *OsMYC2*-overexpressing rice plants is caused by OsNAP-like-responsive genes.

To investigate the direct regulation of *SAG*s by OsMYC2 in vivo, we performed ChIP analysis using the anti-OsMYC2 antibody. It has been revealed that MYC-type TFs can recognize G-box (5′-CACGTG-3′ and 5′-CACATG-3′) and G-box-like (5′-CANNTG-3′) sequences in the promoters of target genes (Abe et al. 1997; Boter et al. 2004; Yadav et al. 2005; Cai et al. 2014). Further, it has been reported that AtMYC2 and OsMYC2 recognize four motifs: 5′-CATGTG-3′ (referred to as G1), 5′-CATATG-3′ (referred to as G2), 5′-CACGTG-3′ (referred to as G3), and 5′-CACATG-3′ (referred to as G4) (Abe et al. 1997; Boter et al. 2004; Dombrecht et al. 2007; Hong et al. 2012; Kazan and Manners 2013; Cai et al. 2014; Uji et al. 2016). We identified some putative G-box/G-box-like motifs (G1–G4) that were recognized by OsMYC2 in all the promoters of the *OsMYC2-responsive genes* (approximately 2.0 kbp) (Fig. 3a). After immunoprecipitation with anti-OsMYC2 antibody, enrichment of specific promoter fragments in the precipitants was determined by qPCR (Fig. 3a). Normal IgG was used as a negative control. As a positive control, the known OsMYC2-recognized region in the promoter of *OsJAZ10* (Uji et al. 2016) was also amplified (Fig. 3b). The results showed that the two G-box/G-box-like regions in the promoters of *similar to SAG*, and one in that of *OsSAG12* had significantly stronger enrichment of OsMYC2 (Fig. 3b). Non-G-box and other G-box/G-box-like regions in these promoters were not amplified (Fig. 3b). In contrast, not all G-box/G-box-like regions in the promoters of the other OsMYC2-responsive *SAG*s were amplified after immunoprecipitation with anti-OsMYC2 antibody (Fig. 3b). These results suggest that OsMYC2 directly regulates the expression of *similar to SAG* and *OsSAG12* in rice.

We have previously demonstrated that OsMYC2 plays an important role in JA-induced resistance to *Xoo*, presumably due to the upregulation of some defense-related genes (Uji et al. 2016). In this study, we further demonstrated that OsMYC2 was also involved in regulation of leaf senescence. Furthermore, we showed that OsMYC2 directly regulated the expression of *similar to SAG* and *OsSAG12* in vivo and indirectly regulated the expression of some *SAG*s including OsNAP-like protein. The role of the OsNAP-like protein in leaf senescence of rice has not yet been studied. Detailed analysis of the newly identified OsMYC2-OsNAP-like pathway might provide further insights into the molecular mechanism of OsMYC2-mediated leaf senescence in rice.

Author contribution statement KG designed the research project. YU performed the research and wrote the paper. KA modified the manuscript. All authors reviewed and approved the manuscript.

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