

## Auxin-responsive *SAUR39* gene modulates auxin level in rice

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The signaling molecule auxin plays a central role in several aspects of plant growth and developmental processes. Underlying optimization of these processes are complex mechanisms orchestrating the expression of genes involved in controlling auxin level, movement and signalling. The small auxin-up RNA (SAUR) family comprises a large set of genes whose expressions are early auxin-responsive. However, the function of these genes is largely unknown. Loss-of-function mutants in a number of Arabidopsis *SAUR* genes did not show any marked phenotypic differences to wild-type plants likely due to compensatory functions of conserved members of the SAUR gene family. We have recently shown that a rice *SAUR39* gene negatively regulates auxin synthesis and transport in rice. Here we propose a model that constitutive induction of *SAUR39* gene expression reduces growth and seed yield in rice plants due to the presence of a lower auxin level, reduced polar auxin transport, less chlorophyll and increased sugar and anthocyanin contents. In wild-type plants, the *SAUR39* gene is expressed at a low level and is transiently induced by changes in external auxin or other environmental stimuli, but within hours of this change its expression is reduced to the low constitutive level. This homeostatic mechanism is essential for optimal plant growth and seed yield and its disruption due to the constitutive overexpression of *SAUR39* leads to a set of negative pleiotropic phenotypes.

includes the regulation of genes from three different early auxin-responsive gene families, through the rapid and transient induction of these genes in response to exogenous auxin supply. These gene families are auxin/indoleacetic acid (Aux/IAA), Gretchenhagen-3 (GH3) and small auxin-up RNA (SAUR).<sup>3</sup> Several genes from the Aux/IAA and GH3 families have been functionally characterized. However, the function of any *SAUR* gene remained unknown.<sup>4</sup> Several unsuccessful previous attempts were made to find functional phenotypes in loss-of-function mutants in different *SAUR* genes. This could be due to several reasons such as functional redundancy and a compensatory role through other mechanisms.<sup>4-6</sup> Most of these functional analysis studies were done in the model plant Arabidopsis which has 78 *SAUR* genes ([www.arabidopsis.org/](http://www.arabidopsis.org/)).<sup>5,6</sup> A large number of these genes are located in tandem with high sequence similarity and identity at the cDNA and amino acid levels amongst them, with the potential for them having overlapping functions. In rice there are 58 *SAUR* genes and most of the genes are staggered on different chromosomes, except for the clustering of some genes on chromosome number 9.<sup>4</sup> However, the sequence identity and similarity among rice *SAUR* genes is less when compared to the Arabidopsis *SAUR* genes. Therefore, there is a higher probability of finding some *SAUR* genes in rice that have unique functions.

In our microarray analysis conducted under different nitrogen regimes in rice, one *SAUR39* (Os09g0545300 or LOC\_Os09g37330.1) gene was induced by changing nitrogen levels.<sup>7</sup> In addition, this gene was also upregulated by transient application of cytokinin, anoxia, and salt stress (Gene expression omnibus profiles,

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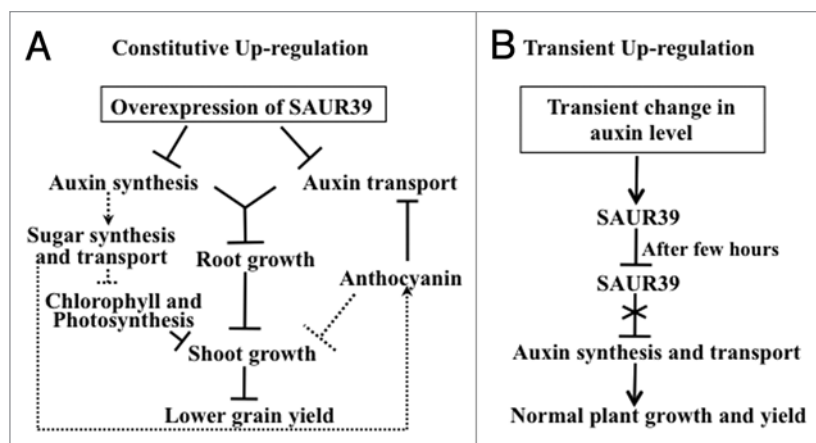
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Auxin plays a key regulatory role for optimal plant growth and development by modulating the expression of genes involved in several physiological processes.<sup>1-3</sup> This



**Figure 1.** A model to explain *SAUR39* gene function in negative regulation of auxin level in rice plants. (A) Constitutive upregulation of *SAUR39* results in reduced rice plant growth and yield via reduced auxin synthesis and transport. (B) Transient change in auxin level results in temporary induction of *SAUR39*. The pointed arrows indicate positive regulation and blunt end arrows indicate negative regulation. Dotted lines indicate putative regulation.

www.ncbi.nlm.nih.gov/) and was also responsive to exogenous auxin supply.<sup>7</sup> The transgenic lines overexpressing this *SAUR39* were developed using a constitutively expressed ubiquitin promoter and interestingly these overexpresser plants were smaller and had less vegetative growth and lower yield as compared to wild-type plants.<sup>7</sup> A model for the role of *SAUR39* gene in this effect is shown in Figure 1 and the reasoning behind consists of the following. The free Indole-3-acetic acid (IAA) level in overexpresser plants was lower than wild-type which could be due to negative feedback inhibition by the constitutively induced *SAUR39* gene. In contrast, in wild-type plants, the *SAUR39* gene likely is repressed due to the presence of destabilizing elements in 3' UTR region, whereas under the constitutive induction of the *SAUR39* gene the plant might sense a sufficient auxin level and give signals to produce less auxin. In turn, a lower auxin level would lead to an increased sugar level which would repress the expression of photosynthetic genes and chlorophyll production (Fig. 1A). An inverse relation between a lower auxin level and higher sugar content in *Arabidopsis* has been reported by Ohto et al.<sup>8</sup> Furthermore, higher sugar levels in plants can repress several genes associated with photosynthesis and induce genes associated with anthocyanin accumulation.<sup>9-11</sup> Less chlorophyll and downregulation of photosynthetic genes in overexpresser plants resulted in lower shoot growth as compared

to wild-type plants (Fig. 1A). Higher sugar content is thought to increase anthocyanin content in plants (Fig. 1A).<sup>8,11</sup> The higher anthocyanin contents are known to repress auxin transport in *Arabidopsis*<sup>12</sup> and the auxin transport was also lower in *SAUR39* overexpresser plants.<sup>7</sup> The lower auxin level and transport would result in less lateral root formation in plants.<sup>1,2,13</sup> Reduced shoot and root growth ultimately resulted in lower seed yield in *SAUR39* overexpresser plants compared to wild-type (Fig. 1A). In wild-type plants the expression of *SAUR39* could be transiently induced by exogenous auxin supply but returns to the normal level after 24 h.<sup>7</sup> The negative feedback regulation of auxin synthesis and transport by the transiently induced *SAUR39* gene would be relieved once the *SAUR39* transcript returns to its baseline level (Fig. 1B). As mentioned earlier, the expression of the *SAUR39* gene can be induced by other environmental stimuli such as anoxia, salinity and application of cytokinin. The prolonged or recurring exposure of plants to these conditions could induce the *SAUR39* gene for a longer period and would possibly lead to a similar downregulation of auxin synthesis and transport and lower growth and yield as was observed in *SAUR39* overexpresser plants. Therefore, a detailed understanding of the molecular mechanisms of this and other *SAUR* genes would shed light on the involvement of *SAUR* genes in auxin signalling and their involvement in feedback

regulation of the auxin level in plants. This future proposed work might include: (1) understanding the role of *SAUR* genes via interaction with calmodulin genes, since the expression of several Ca<sup>2+</sup>-binding/calmodulin genes was higher in *SAUR39* overexpresser plants<sup>7</sup> and some *SAUR* proteins have been shown to bind with Ca<sup>2+</sup>-binding/Calmodulin proteins<sup>14</sup> (2) study the interaction of *SAUR* proteins with other auxin-induced and auxin response factor proteins (3) identification of other *SAUR* genes through transcript profiling in response to different growth conditions and functional characterization of gain-of-function and loss-of-function plants of these genes to identify their unique and non-overlapping functions in various tissues or whole plants.

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