

## PHOTOSYNTHESIS

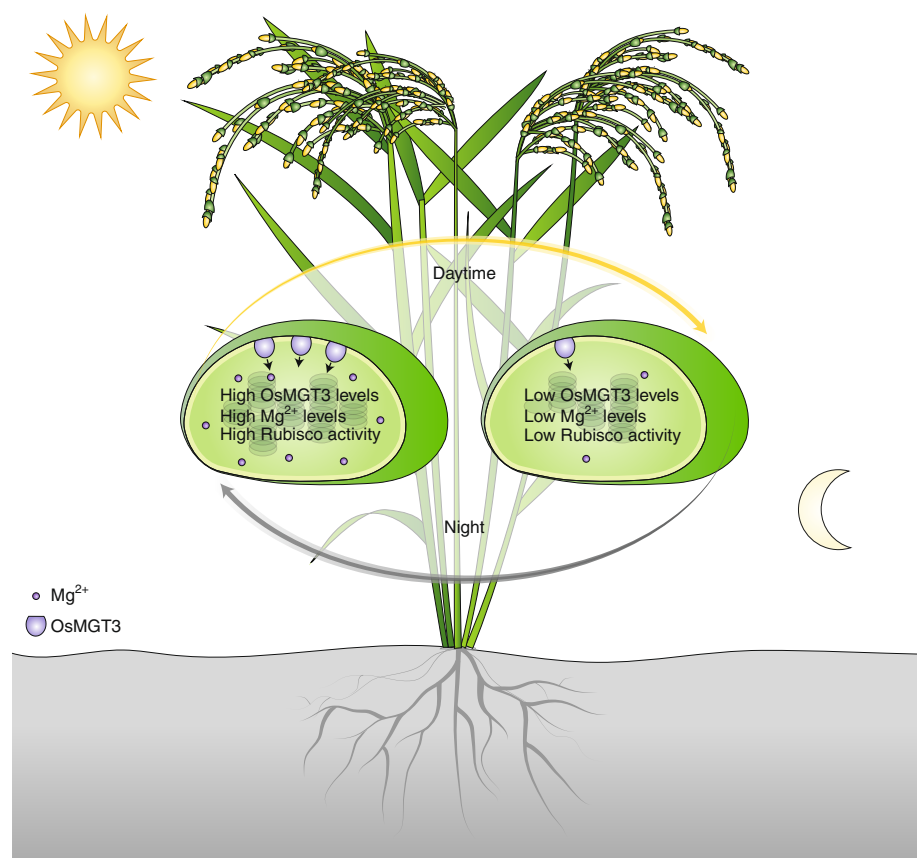
## Rhythms of magnesium

The diel cycle controls the rhythmic changes in photosynthesis. Now, magnesium levels in the chloroplast are shown to follow a diurnal rhythmic change, and a transporter appears to facilitate such a fluctuation, thereby fine-tuning plant photosynthesis on a diel basis.

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With the Earth's rotation on its axis every 24 h, most organisms on the planet have evolved an internal biological clock that governs physiology in the pattern of diurnal rhythms. In plants, miniature solar factories called chloroplasts operate at high intensity during the daytime to convert sunlight into chemical energy as well as carbon dioxide ( $\text{CO}_2$ ) into sugars through photosynthetic reactions; during the night, this system is tuned down. It is generally believed that photosynthesis is controlled by the circadian clock to ensure optimal plant productivity<sup>1</sup>. Meanwhile, due to the dominance of photosynthesis in the primary metabolism of green cells, other plant activities, such as stomatal movement and nutrient mobilization, are often synchronized with the rhythms of photosynthesis. Notably, nutrient acquisition and distribution in plants are also subjected to the circadian control, enabling plant adaption to daily environmental fluctuations that may influence cellular metabolism and physiology<sup>2</sup>. Among multiple mineral nutrients, magnesium ( $\text{Mg}^{2+}$ ) plays a particularly important role in photosynthesis by serving as a central atom for chlorophyll, a counter cation for adenosine triphosphate (ATP) and an indispensable cofactor for photosynthetic enzymes. Although a varying temporal demand for  $\text{Mg}^{2+}$  is assumed to occur in the chloroplast, the circadian regulation of  $\text{Mg}^{2+}$  transport and its possible role in plant photosynthesis remain unknown. In this issue of *Nature Plants*, Li and colleagues<sup>3</sup> reported that  $\text{Mg}^{2+}$  content in the chloroplast stroma of rice mesophyll cells represents a critical checkpoint for coupling the circadian rhythms to plant photosynthesis.

In order to evaluate the physiological role of  $\text{Mg}^{2+}$  in photosynthesis, the authors initially monitored several photosynthetic parameters in response to  $\text{Mg}^{2+}$  deficiency treatment in rice plants. They found that during the early stage of  $\text{Mg}^{2+}$  starvation, photosynthetic light reactions were not affected, whereas the capacity of  $\text{CO}_2$



**Fig. 1 | OsMGT3 mediates  $\text{Mg}^{2+}$  transport into the rice chloroplast and contributes to photosynthetic carbon assimilation on a diel basis.** OsMGT3 is a  $\text{Mg}^{2+}$  transporter localized to the chloroplast envelope of rice mesophyll cells. It facilitates  $\text{Mg}^{2+}$  loading into the chloroplast stroma. Because OsMGT3 exhibits a diel oscillatory pattern in gene expression, it controls the diel fluctuation of  $\text{Mg}^{2+}$  levels in the chloroplast. In the daytime, when OsMGT3 is abundant, chloroplast  $\text{Mg}^{2+}$  levels are high, leading to robust Rubisco activities; by contrast, in the night, a low level of OsMGT3 results in limited  $\text{Mg}^{2+}$  concentrations and Rubisco activities in the chloroplast. This pattern of diel changes in the chloroplast stroma accounts for circadian oscillation of  $\text{CO}_2$  fixation, and therefore partly contributes to circadian rhythms of photosynthesis that influences rice growth and yield.

fixation was significantly decreased. More importantly, they also found that  $\text{Mg}^{2+}$  content in the chloroplast exhibited an oscillatory pattern that was highly correlated with the rhythmic change of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity in vivo. Because  $\text{Mg}^{2+}$

is known to function as a key cofactor of Rubisco, the primary rate-limiting enzyme involved in  $\text{CO}_2$  fixation, this result suggests that diurnal  $\text{Mg}^{2+}$  oscillations in the chloroplast is likely linked to the circadian rhythms of photosynthesis in terms of  $\text{CO}_2$  fixation.

Taking advantage of a specific transport inhibitor in the  $Mg^{2+}$  uptake assay, the authors suggested that the CorA-type  $Mg^{2+}$  transport system may be responsible for the  $Mg^{2+}$  translocation into rice chloroplast. The CorA-type  $Mg^{2+}$  transporters have been found to be ubiquitously present in all organisms. In plants, this family of highly conserved members, termed  $Mg^{2+}$  transporters (MGT; also named MRS2), plays a crucial role in diverse  $Mg^{2+}$  transport processes<sup>4,5</sup>. To identify the particular MGT member in charge of rhythmic  $Mg^{2+}$  transport into rice chloroplasts, the authors analysed expression profiles of all the MGT genes encoded in the rice genome. Among the nine candidates, *OsMGT3* displayed a unique rhythmic expression pattern in leaf blades, which is specifically induced by external  $Mg^{2+}$  availability. Subsequent characterization indicated that *OsMGT3* protein is localized to the chloroplast envelope of leaf mesophyll cells, reminiscent of previous studies on the MGT10 homologue in *Arabidopsis*<sup>6,7</sup>. Li et al.<sup>3</sup> further showed that *OsMGT3* could mediate  $Mg^{2+}$  uptake into bacteria, yeast and animal cells, verifying its role as a functional  $Mg^{2+}$  transporter.

Based on genetic analysis using *osmgt3* loss-of-function mutants, *OsMGT3* appears to be required for maintaining the normal oscillation of  $Mg^{2+}$  levels in rice chloroplasts. Consistent with this conclusion, *osmgt3* mutants were stunted in their growth as compared to wild-type plants, which could be attributed to reduced Rubisco activity and thus compromised capacity of

carbon assimilation observed in the mutant plants. Although circadian oscillation of  $CO_2$  fixation has been well documented as a part of rhythmic photosynthesis, the regulatory basis is enigmatic. A previous study excluded the possibility that rhythmic stomatal opening plays a role, because net  $CO_2$  fixation still oscillates when intracellular  $CO_2$  concentration and stomatal conductance remain constant<sup>8</sup>. The study by Li et al.<sup>3</sup> herein pinpoints a crucial role of an organelle metal transporter in this process: the rhythmically expressed  $Mg^{2+}$  transporter *OsMGT3* in the chloroplast envelope controls the oscillation of  $Mg^{2+}$  levels in the stroma, which contribute to the circadian regulation of Rubisco activity and  $CO_2$  fixation in photosynthesis (Fig. 1). Also important is the finding that transgenic rice plants with increased *OsMGT3* expression in mesophyll cells showed better growth performance in biomass production than their non-transgenic siblings. In these transgenic plants,  $Mg^{2+}$  uptake into the chloroplast was significantly enhanced, concomitant with higher Rubisco activity and an accelerated net photosynthetic rate. If field trials validate this trait, genetic modification of *OsMGT3* may provide a new avenue to engineering plants with higher photosynthetic rate and grain yield.

In a broader context of biology,  $Mg^{2+}$  concentration also fluctuates along the circadian rhythms in both unicellular alga and human cells, which is proposed to play an important role in cellular timekeeping and energy balance over a daily cycle<sup>9</sup>.

Taken together with the study by Li et al.<sup>3</sup>, it is attempting to envisage that cellular and subcellular  $Mg^{2+}$  oscillations may occur as common mechanisms to regulate diverse biological functions in many other systems yet to be researched. Future studies are also required to unravel the coding mechanisms of these  $Mg^{2+}$  oscillations that may involve multiple components. For instance, in addition to *OsMGT3* identified in this study, other  $Mg^{2+}$  transporters and regulatory proteins are likely to work together in shaping up  $Mg^{2+}$  oscillations in the chloroplast. □

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## Competing interests

The authors declare no competing interests.