

# Calcium Signaling is Involved in Negative Phototropism of Rice Seminal Roots

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**Abstract:** Calcium ions ( $\text{Ca}^{2+}$ ) act as an intracellular second messenger and affect nearly all aspects of cellular life. They are functioned by interacting with polar auxin transport, and the negative phototropism of plant roots is caused by the transport of auxin from the irradiated side to the shaded side of the roots. To clarify the role of calcium signaling in the modulation of rice root negative phototropism, as well as the relationship between polar auxin transport and calcium signaling, calcium signaling reagents were used to treat rice seminal roots which were cultivated in hydroculture and unilaterally illuminated at an intensity of 100–200  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$  for 24 h. Negative phototropism curvature and growth rate of rice roots were both promoted by exogenous  $\text{CaCl}_2$  lower than 100  $\mu\text{mol}/\text{L}$ , but inhibited by calcium channel blockers (verapamil and  $\text{LaCl}_3$ ), calcineurin inhibitor (chlorpromazine, CPZ), and polar auxin transport inhibitor (N-1-naphthylphthalamic acid, NPA). Roots stopped growing and negative phototropism disappeared when the concentrations increased to 100  $\mu\text{mol}/\text{L}$  verapamil, 12.500  $\mu\text{mol}/\text{L}$   $\text{LaCl}_3$ , 60  $\mu\text{mol}/\text{L}$  CPZ, and 6  $\mu\text{mol}/\text{L}$  NPA. Moreover, 100  $\mu\text{mol}/\text{L}$   $\text{CaCl}_2$  could relieve the inhibition of  $\text{LaCl}_3$ , verapamil and NPA. The enhanced negative phototropism curvature was caused by the transportation of more auxin from the irradiated side to the shaded side in the presence of exogenous  $\text{Ca}^{2+}$ . Calcium signaling plays a key role as a second messenger in the process of light signal regulation of rice root growth and negative phototropism.

**Key words:** calcium signaling; polar auxin transport; calcium channel blocker; second messenger; negative phototropism

Light is an important environmental factor that controls plant growth and development. Plants respond to light signals such as intensity, quality, and direction using their photoreceptors and light signal transduction pathways, resulting in modifications to metabolism, organogenesis, morphology, and tropism (Pepper et al, 2001; Martin-Tryon and Harmer, 2008). Research on phototropism (bending towards the light source) has had far-reaching consequences in the field of aerial plant parts such as shoots and leaves, but little is known about plant roots, the ‘hidden-half’. In recent years, the seminal, secondary, and lateral roots of a variety of plants have been shown to be negatively phototropic (Okada and Shimura, 1992; Vatha et al, 2000; Briggs et al, 2001; Wang et al, 2002; Mo et al,

2004). Moreover, Wang et al (2002) and Mo et al (2004) found that negative phototropism was induced by blue but not red light. Further investigation revealed that this process involved polar auxin transport, as blue light promoted the transportation of auxin from the irradiated side to the shaded side, resulting in a high concentration of auxin at the shaded side which inhibits growth (Wang et al, 2002; Mo et al, 2004).

Calcium ion ( $\text{Ca}^{2+}$ ) as a second messenger plays an important role in signal transduction and regulates plant development (White, 2000; Wang et al, 2004; Hepler, 2005; Volotovski, 2011). Several lines of evidence have elucidated the relationship between  $\text{Ca}^{2+}$  and gravitropism of plant roots (Björkman and Leopold, 1987; Toyota et al, 2008). For example, the root tips of corn and oat did not undergo gravitropism when they were treated with the calcium chelates ethylene diamine tetraacetic acid (EDTA) or ethylene glycol

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tetraacetic acid (EGTA) (Lee et al, 1983a; Daye et al, 1984). Moreover, when roots were placed in a horizontal position, the concentration of  $\text{Ca}^{2+}$  in the downside of root tips increased (Lee et al, 1983b; Björkman and Cleland, 1991). In response to gravity, a bending of the root towards the gravity was observed (Gehring et al, 1990; Monshausen et al, 2011).

Polar auxin transport also has a major role in root gravitropism (Björkman and Leopold, 1987). Previous investigation showed that exogenous auxin enhanced the  $\text{Ca}^{2+}$  concentration in the cytoplasm (Felle, 1988; Gehring et al, 1990), while Hepler and Wayne (1985) found that auxin induced a change of  $\text{Ca}^{2+}$  level in the plasma membrane in root gravitropism. However, there have been few reports about the interaction between auxin and calcium signal transduction on the negative phototropism of plant roots.

Therefore, the present study aimed to investigate the effect of auxin and calcium signal transduction on negative phototropism of rice roots using calcium signaling reagents such as  $\text{CaCl}_2$ , calcium channel blockers ( $\text{LaCl}_3$  and verapamil), calcineurin inhibitor (chlorpromazine, CPZ), and polar auxin transport inhibitor (N-1-naphthylphthalamic acid, NPA) to treat rice seminal roots and to measure the negative phototropism curvature and growth rate.

## MATERIALS AND METHODS

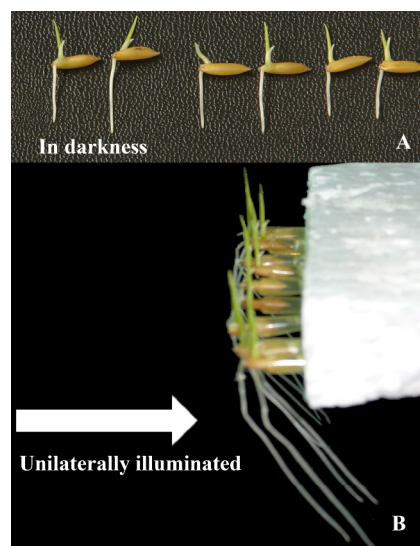
Rice (*Oryza sativa* L.) cultivar Yangdao 6 (indica) was used as the experimental material. All reagents (Sigma Chemical Co., St. Louis, USA) were chromatographic pure grades.

### Cultivation of seminal roots

Pre-germinated rice seeds were selected to cultivate seminal roots using the water culture method in which rice seeds were placed in the plastic head of quantitative pipette with the germ of the seed outside. The plastic heads were then inserted into a foam plate which was placed in a glass tank containing water (Fig. 1). Vertical seminal roots with 4–7 mm in length were cultured for 24 h with unilateral light (Fig. 1). The cultivation was performed in an artificial climate chamber at 30 °C and with a relative humidity of 75%.

### Treatment of seminal roots

$\text{CaCl}_2$  (0, 0.02, 0.05, 0.10, 0.20 and 0.50 mmol/L),  $\text{LaCl}_3$  (0, 3.125, 6.500, and 12.500  $\mu\text{mol/L}$ ), verapamil (0, 25, 50, 75, 100 and 125  $\mu\text{mol/L}$ ), CPZ (0, 5, 10, 20



**Fig. 1. Fixed mode and results of unilateral illumination of rice seminal roots.**

A, Rice seminal roots in dark; B, 24 h after unilateral illumination.

and 40  $\mu\text{mol/L}$ ) and NPA (0, 2 and 4  $\mu\text{mol/L}$ ) were used as treatments of seminal roots, respectively. All reagents were mixed in 1/10 Hoagland medium, with 0  $\mu\text{mol/L}$  reagent as the control (CK). Unilateral light intensity ranged from 100 to 200  $\mu\text{mol}/(\text{m}\cdot\text{s})$ . Negative phototropism curvature and growth rate were determined after roots cultivated for 24 h.

### Determination of auxin content in root tips

Indole-3-acetic acid (IAA) is the most widespread representative plant auxin. Under low temperature and weak light conditions, a 4-mm section of root tip was cut longitudinally into two parts, the irradiated side and shaded side, representing parts that were exposed to light and kept shaded, respectively. A 0.5 g section of each part was taken to determine the IAA content using an enzyme-linked immunosorbent assay (ELISA) (Mo et al, 2004).

## RESULTS

### Effects of $\text{CaCl}_2$ concentration on negative phototropism curvature and growth rate of rice seminal roots

The negative phototropism curvature and the growth rate of rice seminal roots were both promoted by  $\text{CaCl}_2$  solution with a concentration lower than 100  $\mu\text{mol/L}$ , but were inhibited by higher concentrations. The greatest promoting effect was seen with 50  $\mu\text{mol/L}$

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