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News and Views

A matter of time: Red light regulation of APYRASES shapes seedling growth during de-etiolation

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When growing in the absence of light, for example when a seed germinates belowground, the emerging seedling must tightly manage its limited resources until it can establish an autotrophic lifestyle. Hypocotyl growth is prioritized over root elongation, the cotyledons close, and the apical tip of the seedling bends in the shape of a hook to protect stem cells. The morphological features of dark-grown seedlings maximize their chances to emerge from the soil and reach the light (de Wit et al., 2016).

As soon as seedlings detect red light (R), seedlings adjust their growth as part of a process known as de-etiolation. Hypocotyl elongation is quickly arrested, the apical hook opens, cotyledons expand, and root growth is promoted (de Wit et al., 2016; Figure 1). De-etiolation involves multiple molecular players, such as APYRASE (ATP-diphosphatase, APY) 1 and APY2 in Arabidopsis (*Arabidopsis thaliana*; Wu et al., 2007). APY activity has been linked to the control of auxin transport (Liu et al., 2012) and the repression of genes encoding enzymes that strengthen cell walls (Lim et al., 2014). After a few minutes of R irradiation, the level of *APY* transcripts and APY proteins quickly declines, which coincides with the arrest of hypocotyl elongation (Wu et al., 2007). However, the results in this previous report were based on the analysis of the whole above ground portion of seedlings treated with a short time of R exposure. As APY accumulates in fast-growing tissues (Wu et al., 2007), and long R treatments promote the growth of cotyledons and roots, a question arises: Does R control APY differently among seedling organs or time points?

In this issue of *Plant Physiology*, Weeraratne et al. (2022) measured the levels of *APY1* and *APY2* transcripts and proteins in different tissues of etiolated seedlings at multiple points after R irradiation. They found that APY protein accumulation generally coincides with the effect of R on growth (Figure 1). Using an anti-APY antibody that detects both APY1 and APY2 (Wu et al., 2007), the authors showed that APY protein levels increased gradually in the apical hook and cotyledons starting after 4 h of R treatment, and continuing until the last sampling point (72 h). The dynamics of APY accumulation followed that of R-induced hook opening and cotyledon expansion. The hook opened after 1–12 h of R treatment, while cotyledon area approximately doubled between 24 h and 48 h and continued to increase from 48 h to 72 h after treatment. Interestingly, *APY* mRNA levels did not increase in response to R, suggesting that R controls APY levels in hooks and cotyledons by increasing translation and/or decreasing protein turnover. The exact mechanism needs further research.

When seedlings grow in a medium containing sucrose, R treatment slows root growth during the first 12 h (Correll and Kiss, 2005), but at later time points, root growth is actually promoted (Kircher and Schopfer, 2012). Coincidentally, R treatment lowered APY protein levels after 6–12 h of treatment, but both gene expression and protein accumulation were upregulated after 24 h (Figure 1).

The authors also found that *APY* genes are required for normal morphological responses to R treatment and darkness. Because *apy1 apy2* double knockout mutants are lethal (Steinebrunner et al., 2003), the authors used estradiol-induced *APY1* silencing in an *apy2* mutant background (Wu et al., 2007). Upon estradiol treatment, the *APY1* mRNA levels decreased by 70% (Lim et al., 2014). De-etiolation responses in this line were reduced, as hook opening and growth of cotyledons and roots were attenuated compared

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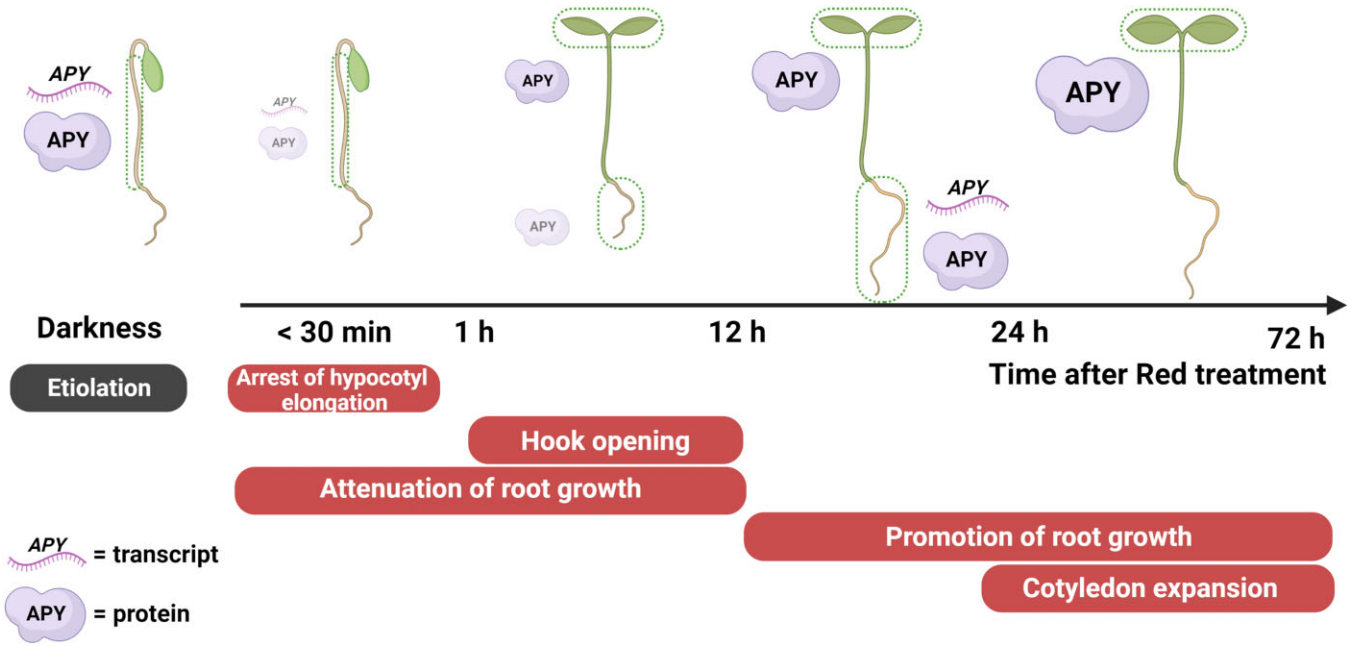

Figure 1 Red light regulation of APY levels during de-etiolation across seedling organs. *APY* mRNAs and APY proteins accumulate in fast growing tissues, such as the hypocotyl of etiolated seedlings (Wu et al., 2007). After short times of red light (R) irradiation, hypocotyl growth is arrested, which coincides with the suppression of APY levels in this organ (Wu et al., 2007). R treatment promotes a gradual increase in APY proteins in the apical hook and cotyledons, which matches the dynamics of hook opening and cotyledon expansion. Root growth is initially attenuated by R (Correll and Kiss, 2005) but then enhanced at later points (Kircher and Schopfer, 2012). Coincidentally, R lowers APY proteins levels after 6–12 h of treatment, but both gene expression and protein accumulation are upregulated after 24 h. Tissues where APY transcripts and proteins were measured are enclosed with dotted lines. Created with BioRender.com.

to wild type after R treatment. On the contrary, in *APY1* or *APY2* overexpressors, the apical hook of seedlings grown in the dark was more open than that of wild-type plants.

Together, the results of Weeraratne et al. (2022), in combination with the previous report of Wu et al. (2007), highlight the key role of APY in mediating R regulation of growth during de-etiolation. Future research may address how R controls APY levels across organs in apparently opposite ways, promoting protein accumulation in expanding tissues, such as the cotyledons, and lowering protein accumulation in the hypocotyl, where growth is arrested. Time will tell.

Conflict of interest statement. None declared.

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