Adapting to High Light: At a Different Time and Place?

When rays of light enter a plant cell, they find their way to the chlorophyll pigments located in the chloroplast. Chlorophyll molecules are embedded in the light reaction complexes PSI and PSII, which capture and store the energy needed for carbon fixation in the Calvin cycle. In an ideal situation (and textbooks), the constant excitation of chlorophyll causes a continuous energy supply that makes the Calvin cycle run smoothly. However, as more often is the case, plants deal with a far from ideal situation. Outside of the laboratory, many factors affect the efficiency of the photosynthesis reaction: water and CO_2 limitations, heat, cold, and fluctuations in light availability. Plants experience changes in light quality (sunrise, sunset, shading of other plants) and quantity (clouds, sun flecks, nights) on a daily and seasonal basis. Many growth and developmental adaptations to changes in the light environment are mediated by photoreceptors that sense specific wavelengths. Phytochromes and cryptochromes mediate shade-avoiding phenotypes, and phototropins induce chloroplast movements to avoid high light (Kagawa et al., 2001; Fraser et al., 2016). However, changes in light quantity are also rapidly sensed by the light reaction complexes within the chloroplasts.

A sudden high photon flux can be stressful and cause damage to the chloroplasts. It results in a disbalance between the light reactions and Calvin cycle, which leads to rapid acidification of the thylakoid membranes. In addition, if excited chlorophyll cannot release its energy to photochemical reactions, it can transfer it to O_2 molecules, which results in singlet oxygen, a damaging reactive oxygen species. To prevent this, part of the excess excitation energy is released as heat via non photochemical quenching (Müller et al., 2001). Prolonged exposure to high light levels will ultimately reset photosynthetic capacity to adapt the plant to the new environment. Both short- and long-term adaptations to increased light intensity require physiological and molecular changes in the chloroplast, but the regulation of these changes is still poorly understood.

The work of Schuster et al. (2020) published in this issue of *Plant Physiology*, aimed to understand to what extend tobacco (*Nicotiana tabacum*) seedlings alter transcription and translation of chloroplast genes during rapid adaptation to high light. As chloroplasts have an endosymbiotic origin, they have their own DNA and protein synthesis machinery. Although most proteins required for chloroplast function are encoded in the nucleus, some essential proteins are synthesized in the chloroplasts themselves, such as the core subunits of PSII (PsbA) and PSI (PsaA/B). PsbA is especially sensitive to photodamage, and earlier work showed that PsbA synthesis increases with increasing light intensity as a repair mechanism (Chotewutmontri and Barkan, 2018).

However, it remained unknown how physiologically relevant elevations of light intensity regulate genome-wide changes in chloroplast translation. Schuster et al. (2020) used tobacco plants with fully operational chloroplasts and exposed them to an ~3-fold (350–1,000 μmol m^{-2} s^{-1}) or 20-fold (50–1,000 μmol m^{-2} s^{-1}) increase in light intensity. Already after 2 h of high light, the decreased Fv/Fm ratio indicated photoinhibition of PSII, and after longer exposure (2 d), chlorophyll content slightly dropped. However, these physiological changes were not accompanied by substantial changes in gene transcription or translation. The researchers confirmed the previously demonstrated increase in translation of *PsbA*, but this seems to be an exception rather than a rule for the whole chloroplast genome. Considering all the physiological changes that occur during early adaptation to high light stress, it comes as a surprise that these do not require much input from the chloroplast itself. Why are alterations in chloroplast gene expression not involved in rapid adaptations to high light?

The first possible answer to this question is, as stated by the authors, that plasticity is not always beneficial in the short term. Light intensity changes over the course of every day and the constant high light applied here might pose only a minor challenge to plant metabolism. Longer-term acclimation to the new environment will most likely require the synthesis of new photosynthesis complexes.

Another answer to the question lies outside of the chloroplast. As most chloroplast-localized and stress-response proteins are encoded in the nucleus, it is likely that the rapid responses to high light require enhanced transcription of nuclear, but not chloroplast, genes. High light quickly causes the release of reactive oxygen species, which are considered major retrograde (chloroplast-to-nucleus) signals that induce cell-wide responses (Crawford et al., 2018). Indeed, in Arabidopsis (*Arabidopsis thaliana*), the shift to high light causes changes in cytosolic metabolites and translation within seconds to minutes, followed by the release of (plastid-synthesized) hormones and nuclear transcriptional changes within minutes to hours (Dietz, 2015).

The work of Schuster et al. (2020) supports a model in which, even though the photosynthesis

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apparatus is able to rapidly adjust to high light-induced damage, the chloroplast transcription machinery is less quick to respond. The earliest stress seems to be resolved by posttranslational and physiological processes and the hard work of the nucleus, while chloroplast genes are only called upon if the stressful situation becomes the new standard.

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