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► To cite this version:

Guillaume Charrier. Perceiving neighbors to anticipate the struggle for light. *Plant Physiology*, 2021, 186 (4), pp.1760-1761. 10.1093/plphys/kiab260 . hal-03372237

HAL Id: hal-03372237

<https://hal.inrae.fr/hal-03372237>

Submitted on 10 Oct 2021

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Perceiving neighbors to anticipate the struggle for light

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Perception of the local environment (e.g., temperature, light, wind) is essential for plants to shape their form and optimize resource acquisition. As with most stress factors, plants can adopt two contrasting strategies in response to shading: tolerance and avoidance. Shade-tolerant plants are usually slow growing and adapt their photosynthetic structures to optimize light interception at low light levels. Shade-avoiding plants enhance their growth to keep their leaves exposed to high light levels, a change in phenotype called shade avoidance syndrome. Light quantity and quality are two important signals to anticipate the presence of potential competitors (Gundel et al., 2014).

Because photosynthetic pigments strongly absorb photons in the visible wavelength range but almost none in the far-red range, light transmitted from or reflected by neighboring plants is depleted in red (ca. 670 nm) and enriched in far-red (ca. 730 nm). The ratio of red to far-red (R:FR) is detected by phytochromes that can adopt two photointerconvertible forms: the inactive R-light absorbing form and the active FR-light absorbing form. The photoequilibrium of the two forms thus depends on the R:FR ratio. The decrease of the R:FR ratio from 1.15 under natural light to less than 0.5 under the canopy is, therefore, an early signal of light competition before actual shading significantly decreases the irradiance (in the Photosynthetically Active Radiation range PAR, measured mainly by cryptochromes in the blue range, 400–500 nm). Concurrent detection of light quality by the R:FR ratio and fluence allows the plant to distinguish between the threat of shading and actual shading (Franklin and Whitelam, 2018).

In the current issue, Morelli et al. (2021) examined how perception of competing neighbors would modulate photosynthesis and morphology. In shade-avoiding and shade-tolerant species, they manipulated the quantity (PAR) or quality (R:FR ratio) of light to perform light response curves. They measured the light use efficiency of photosystem II

and the corresponding electron transport rate at different light intensities, from darkness to full irradiance. The maximum electron transport rate, maximum quantum efficiency, and the rate of photosynthesis in the light-limited region of the light curve were used as relevant indexes for comparing species and responses to variation in the light treatments.

Reversible changes in the abovementioned photosynthetic parameters, under changing light regimes are called photoacclimation. It is generated by adjustments in various molecules involved in the photosynthetic processes such as pigments, enzymes, protein complexes, and electron transport components (Falkowski and LaRoche, 1991). Photoacclimation compensates for changes in spectral irradiance maintaining a relative efficiency of photosynthesis in response to lower or higher irradiance in shade-avoiding and shade-tolerant species, respectively. Morelli et al. (2021) showed that when shifted to a lower irradiance, shade-tolerant species (e.g., *Cardamine hirsuta*) maintained similar photosynthetic activity whereas shade-avoiding species (e.g., *Arabidopsis thaliana*) exhibited a decrease in photosynthetic efficiency. However, photoacclimation, which is induced by changes in PAR, appeared in some species as a distinct process from elongation that was induced by the low R:FR ratio. This finding was confirmed in mutants in which the main actors promoting elongation, Phytochrome Interacting Factors, were modulated. In *A. thaliana* mutants, Phytochrome Interacting Factors were downregulated, reducing plant sensitivity to low R:FR and its ability to elongate in response to proximity without altering their photoacclimation response to a low PAR. In *C. hirsuta* mutants, Phytochrome Interacting Factors were up-regulated and the plants gained both the ability to elongate in response to proximity and to photoacclimate.

In the shade-avoiding *A. thaliana*, the changes induced by proximity shade were characterized. Low R:FR induced a decrease in photosynthetic pigment levels (chlorophylls and carotenoids) and photosynthetic activity and a

Received May 17, 2021. Accepted May 28, 2021

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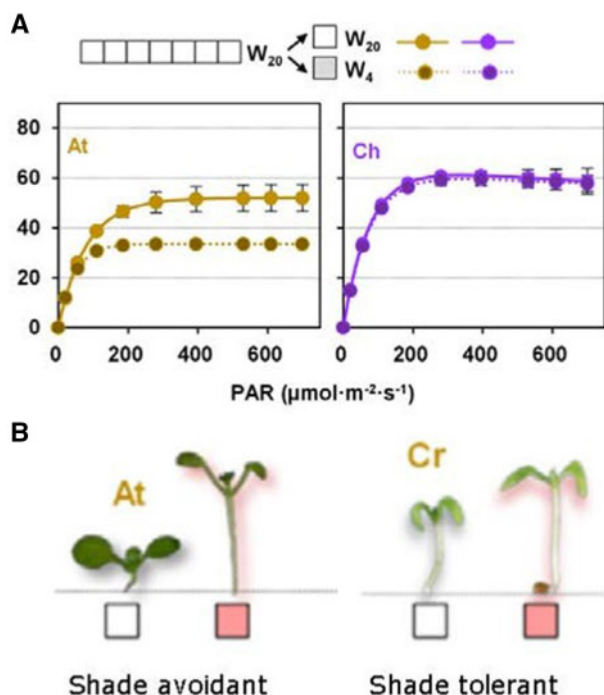


Figure 1 A, Light curves of *A. thaliana* (At, left) and *C. hirsuta* (Ch, right) seedlings germinated and grown under white light (W₂₀) for 7 d and then either kept under W₂₀ or transferred to lower PAR (W₄) for 1 more day. B, Hypocotyl elongation response to low R:FR of *A. thaliana* (At, left) and *C. hirsuta* (Ch, right) germinated and grown under W₂₀ for 3 d and then either kept under W₂₀ or transferred to low R:FR (W₂₀ + FR) for 4 more days (adapted from Morelli et al., 2021).

downregulation of the expression of many genes from different pathways (pigment biosynthesis, photosynthesis, and carbon fixation). In addition, dark respiration became very limited under low light conditions, maintaining a carbon balance close to zero. The ultrastructural changes

observed in chloroplasts were similar to the changes induced by low PAR. Initial exposure to a low R:FR therefore improved the photoacclimation to low PAR, maintaining an efficient photosynthesis under low light.

Light signals modulated by neighboring plants would induce photoacclimation to low PAR in shade-avoiding but not in shade-tolerant plants. To avoid exposure to limiting light, plants must anticipate changes in their environment by perceiving the changes in the R:FR ratio. Indeed, shade-avoiding species must acclimate their photosynthetic machinery to foreseeable shade conditions in order to maintain a high assimilation rate and thus ensure future elongation. The methodological and conceptual advances brought by Morelli et al. (2021) may have profound implications for the ways we think about optimizing light distribution in multispecies and heterogeneous crops, e.g., annual intercropping, agroforestry, or mixed forests.

Funding

This work has been carried out with financial support from the Pack Ambition Recherche program 'Doux-Glace' from the Auvergne-Rhône Alpes region. This work was also supported by the program ANR Acoufollow (ANR-20-CE91-0008) funded by the French National Agency for Research and the Austrian Science Fund.

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