

A lycophyte's plight when the light is too bright

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Plants cannot go to the store to buy sunscreen when they get too much sunlight. Instead, they use a suite of molecular processes that turn excess absorbed light energy into heat so that it can be harmlessly dissipated. These photoprotective processes collectively fall under the umbrella term “nonphotochemical quenching of chlorophyll fluorescence” which is often shortened to “nonphotochemical quenching” or “NPQ.” If excess sunlight is not dissipated via NPQ, it can result in damage and inactivation of the photosynthetic machinery, specifically photosystem II (PSII), that is energetically costly to repair. While many years of research have led to the identification of proteins and pigments involved in NPQ and of different pathways of NPQ, the underlying molecular mechanisms that plants use to dissipate excess light energy still remain unclear.

One possible reason that the mechanisms of NPQ are difficult to work out is because photoprotective heat dissipation is measured indirectly. Instead of measuring the heat generated during this process, researchers measure light that is re-emitted from chlorophyll molecules as fluorescence. Changes in chlorophyll fluorescence that occur in response to illumination are used as a proxy for how much heat dissipation a plant is performing. Developing new methods for obtaining measurements of chlorophyll fluorescence and transforming them into parameters that better reflect levels of photoprotective heat dissipation remains an active area of research. One such method is the measurement of “photochemical quenching measured in the dark” (qP_d) which attempts to determine how much of the observed changes in chlorophyll fluorescence are due to photoinactivation of PSII and how much are due to photoprotective NPQ (pNPQ) (Ruban & Murchie, 2012). However, this new method has produced results that are at odds with other experimental readouts for assessing photoprotection, like measuring bleaching in response to excess light, so additional experimental validation may be required (Bassi & Dall'Osto, 2021).

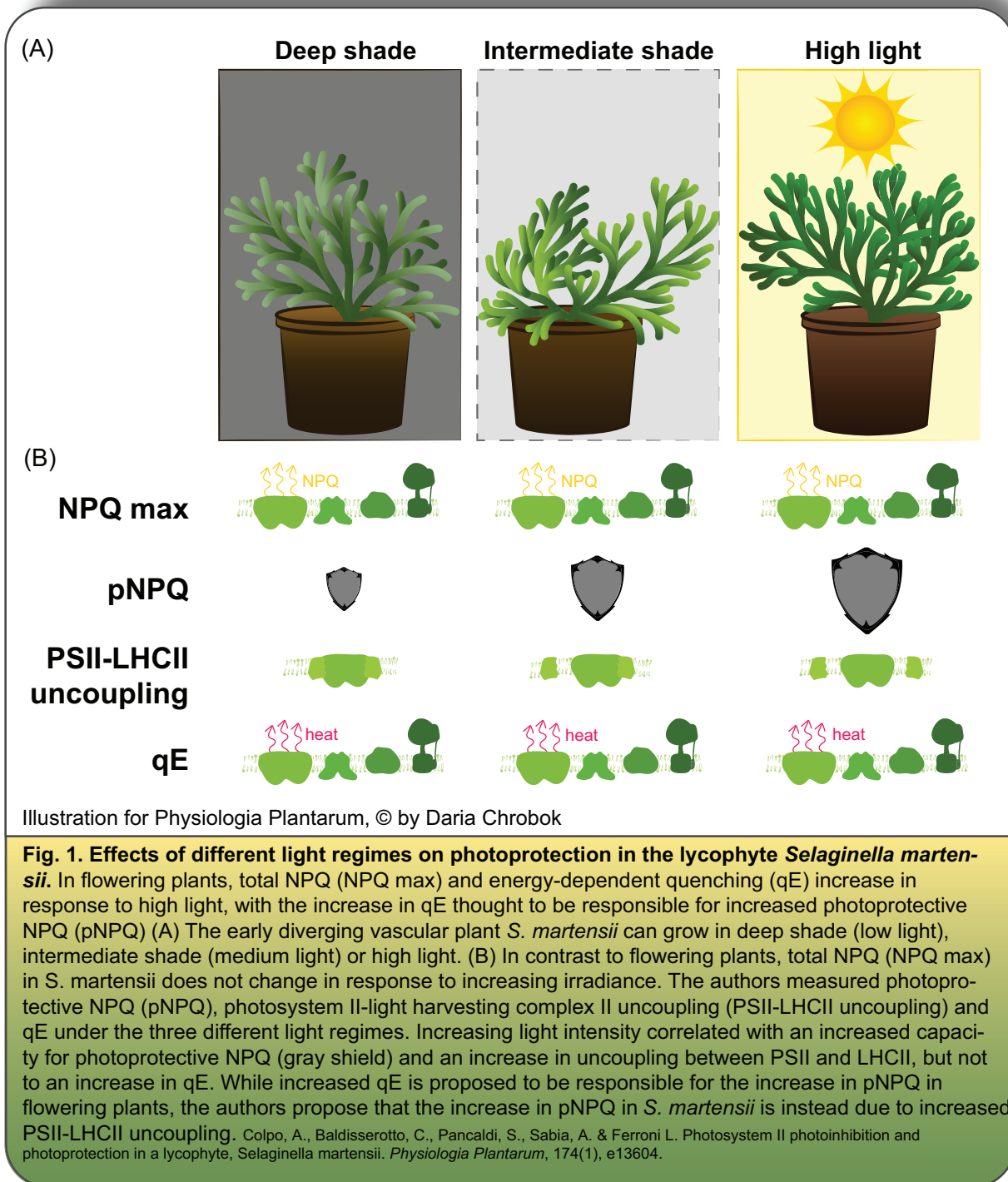
One way to glean more information about the biological meaning of a new method or measurement is to test it on additional model systems. In this issue of *Physiologia Plantarum*, Colpo et al. (2021) have measured qP_d and pNPQ in the lycophyte *Selaginella martensii* after growth in low, medium, or high light (Figure 1). This plant is an interesting choice for testing a new measurement of NPQ because it is evolutionarily situated between two of the best-studied systems (green algae and flowering plants) of the green lineage. Furthermore, *S. martensii* appears to have efficient means of balancing light utilization with energy dissipation as evidenced by its ability to acclimate to and grow under both low and high light (Ferroni et al., 2016).

To put these new measurements to the test, Colpo et al. measured qP_d and pNPQ for low, medium and high light-grown plants and compared their values to previously obtained results showing the stoichiometry, abundance and behavior of photosynthetic protein complexes and NPQ. They found that while plants grown low, medium, and high light exhibited roughly the same maximum capacity for NPQ (NPQ_{max}), those grown under high light display higher levels of pNPQ relative to low and medium light-grown plants (Figure 1). However, the type of NPQ hypothesized to be responsible for increases in pNPQ in flowering plants, called qE, was found to be relatively unchanged between low and high light-grown plants in previous work (Ferroni et al., 2016) so some other factor must be responsible for the observed increase in pNPQ. The authors propose that, at least in *S. martensii*, the increased pNPQ arises at least partially from an increase in the amount of LHCII that are energetically uncoupled from PSII and/or attached to photosystem I (PSI) (Figure 1). They found that differences in LHCII uncoupling also affect the measured values of qP_d but that a slightly different parameter qP_{dhet} , which corrects for LHCII heterogeneity, does indeed reflect the levels of photoinactivated PSII in *S. martensii*.

Overall, the results presented by Colpo et al. help to flesh out a more complete picture of what the parameters qP_d and pNPQ reflect. They also illustrate a perhaps underappreciated role for

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uncoupled LHCII in mediating NPQ, at least in *S. martensii*. All this might feel a bit esoteric (unless you are an NPQ connoisseur), but these results may have far-reaching consequences. NPQ has become a popular target for genetic modification in plants, with some modified lines showing increasing crop yield and productivity (Kromdijk et al., 2016). Developing methods for accurately measuring the components of NPQ is important if these components are to be more precisely modified. Colpo et al. have also shown that

the components of NPQ that are affected by uncoupled LHCII might warrant a closer look and eventually lead to yield-increasing modifications as well.

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