

Photosynthetic Acclimation to the Light Environment: Molecular Mechanisms to Understand Plant Consortia

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Among ecological factors, light has a major influence on the life of land plants. Within natural plant consortia, variations in light intensity (irradiance) and quality (wavelength) are two direct consequences of plant stratification, experienced not only by plant individuals growing at different layers, but even by leaves of the same tree located in different positions of the crown. Two conditions can easily be described, i.e. the “sun condition” and the “shade condition”. With respect to full sunlight, the shade condition is characterized by low irradiance, but is also enriched in the far red spectral range, because most light has already been absorbed by the upper canopy, especially the red component [1,2]. Between these two extremes, there is a gradient of light regimes across the plant consortium. Fluctuations in irradiance (clouds, leaf movements) increase the complexity of description of the light regime to which plants are exposed. A series of processes occur in plants to ensure photosynthesis and prevent photodamage, leading to photoacclimation. Clearly, the problems linked to light energy management depend on the position of a leaf/plant in the consortium. Different mechanisms have been described at the molecular level to explain the functional flexibility of plants with respect to light availability. Some of them occur after exposure of a plant to stable light regimes for hours to days (long term responses, LTR) and are due to modulations of gene expression [3,4]. The thylakoid membrane hosts in fact two photochemical centres, i.e. photosystem I (PSI) and II (PSII), working in series and served each by a complex for light harvesting (LHCI and LHCI) [4]. LTR to shade can be easily monitored, indeed shade leaves normally exhibit larger LHCI and consequently higher chlorophyll content and lower chlorophyll a/b ratio [2,5]. LHCI also plays a fundamental role under full sunlight, which induces the transition of this complex from the “harvesting state” to the “dissipative state”, i.e. a state in which the absorbed light energy is converted safely to heat. This mechanism of photoprotection is known as non-photochemical quenching of chlorophyll fluorescence (NPQ) [6]. Another fundamental role of LHCI is in energy distribution between PSII and PSI, through a process called state transitions [7]. State transitions are mediated by reversible LHCI phosphorylation, which increases affinity of LHCI for PSI with respect to PSII [8]. Today, our understanding of the genetic and biochemical bases of photoacclimation in higher plants is very advanced, mostly using the model organism *Arabidopsis thaliana*. Conversely, there is still a need to contextualize the integration of these processes in natural plant consortia: what is their relevance from an eco-physiological point of view?

In recent years, an interesting proposal has been put forward by Dietzel et al. [9], who suggested that photoacclimation arises from the complementarity of the three types of processes - LTR, NPQ, state transitions -, which operate according to a hierarchy of relevance (and activation time) from sun to shade conditions: sun leaves emphasize photoprotection against light excess through effective NPQ, shade leaves emphasize their light harvesting ability, which is reached through

LTRs. State transitions, though operative for each light condition, could be particularly advantageous to respond to light fluctuations. The operation of state transitions has been demonstrated in experiments using changes in light quality to excite either PSII or PSI. Excitation of PSI is obtained with far red light and promotes association of LHCI with PSII; conversely, if PSII is preferentially excited with red light, LHCI is phosphorylated and associates with PSI [10-12]. The dynamic regulation of such reversible transition occurs in a time-scale of a few minutes and is therefore compatible with a response to light fluctuations [9,12]. Many molecular aspects of state transitions are today known in great detail [10,12-14]. However, there are some non-trivial difficulties in interpreting the eco-physiological significance of state transitions. First of all, in plant consortia, light quality varies from full-spectrum to far-red enriched; no environment enriched in red light exists in nature. Second, it is known that LHCI phosphorylation is low in darkness (potentially similar to far red-light conditions), higher at low light (potentially similar to red-light conditions), but again low at high light intensities [13]. A new idea about the biological meaning of state transitions in connection with NPQ has been elaborated by the group of Eva-Mari Aro [15-17]. It is proposed that, under natural conditions, the interplay of the two mechanisms ensures adequate redox balance in the chloroplast: under low light, phosphorylated LHCI balances the energy to be transferred to PSII and PSI (thus not a prominent transfer to PSI); while, under intense light, NPQ decreases the efficiency of both PSII and PSI antenna systems. Also in this model, focus is on light fluctuations, to be intended as temporary changes in intensity of natural white light, as they may occur in cloudy days. However, when considering understory vegetation layers, the situation is complicated by the enrichment in far red light, which excites preferentially PSI and thus requires a re-equilibration towards PSII. Here, in fact, the background in which state transitions operate is that of the LTR to shade. Interestingly, state transitions and LTR share common points of regulation [18,19].

Whereas basic research looking for an integrated view of the functional flexibility of the photosynthetic apparatus in response to light variations is producing new exciting results and sometimes contrasting views [11,16,17,20], important contributions can come from field

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investigations. Among suitable analysis techniques, the availability of portable pulse amplitude modulated (PAM) fluorimeters gives the opportunity to study photosynthesis and photoprotection under natural field conditions [21]. This has proven to be a powerful approach for the analysis of diurnal and seasonal variations in photosynthetic parameters [22] and can as well be profitably applied to characterize vertical patterns, *i.e.* the expression of LTRs, including different species, different leaves of a single species, up to different portions of the same leaf [23-27]. Nevertheless, evaluations about the impact of light on a vertical pattern of plant species should also take into account that each pattern is also the result of a range of interactions of plants with their environment, thus not only light, but water, nutrients, temperature, biotic interactions. It is also convenient to consider the degree of evolution of species.

What is then the ecological relevance of the current models concerning the interplay between LTR, NPQ and state transitions? To answer this question it is necessary to put to the test their predictions in the field and see in which measure these models are proper descriptors of nature facts.

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