Exploiting heterogeneous environments: how do plants 'decide' to acclimate to a highly variable light input?

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Background

Light is one of the most variable resources for plants and is capable of changes of large magnitude over quite short periods of time. Solar movement, canopy movement, climate and canopy architecture can combine to produce a complex pattern of light in time and space. This has profound consequences for photosynthetic CO_2 assimilation of leaves, which is often slow to respond to the changes in light. In a matter of seconds light can shift from being limiting for photosynthesis to high levels that are sufficient to saturate photosynthesis and risk photooxidative stress. Over the short term the mechanisms that plants use to deal with these changes are relatively well understood. For example there is a balance required between photosynthesis and photoprotective processes.

One area that is not well understood is how photosynthesis in plants responds to changes in light over longer time periods (two or more days usually). 'Acclimation' is a change in the composition of the photosynthetic apparatus to light intensity which improves quantum efficiency under low light and increases the maximum capacity under high light. This optimizes light use in both cases. For example under high light, absorption is not limiting so the amount of light harvesting pigment-protein complex reduces while the level of Calvin cycle enzymes increases [1]. This allows photosynthetic rate to increase. Acclimation to light is a ubiquitous process in plants that enables the efficient exploitation of light and also maintains a high economy of form and function. Acclimation requires gene expression, protein synthesis and degradation and consumes energy and resources.

But light can be highly variable from day to day and hour to hour. Figure 1 shows typical daily variation in light intensity beneath a plant canopy. How do plants and leaves determine that the frequency and/or intensity of high light or low light events is sufficient to induce an acclimation process? This is important because of the metabolic cost involved. For short-term photosynthetic shifts (minutes, seconds) it is possible to invoke enzyme activation state, metabolite level and the state of energisation of the thylakoid membrane as a kind of 'memory' of past light history [3]. What about long term changes (days): do plants accumulate a 'memory' of past high and low light events and if so which features of the variation do they use before a threshold for acclimation is reached? Is it correct to assume that plants somehow determine the probability of future high / low light events?

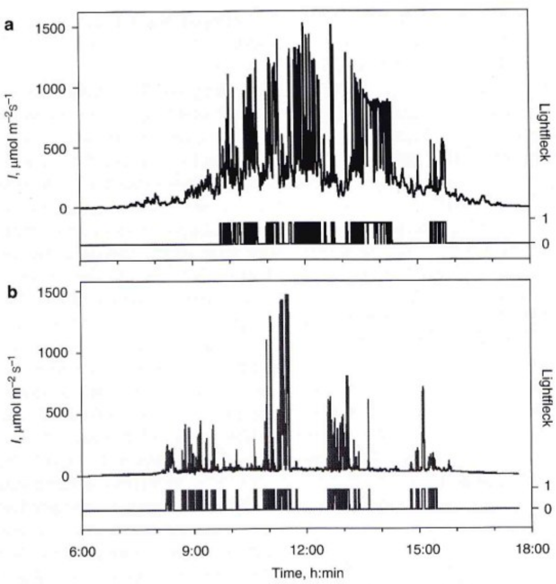


Figure 1. Diurnal course of photosynthetically active radiation in a forest understory. Lightfleck events are shown in the lower part of the graph. From [2].

Example: one can supply the same amount of light as short, bright 'pulses' of light or as a lower, continuous irradiance. These tend to induce different levels of acclimation or none at all if the light is not high enough, or the pulses of light the wrong frequency, length or intensity, acclimation may not occur. The question is: what property of the light supplied is used to induce the acclimation response and how do the signaling components work? There are surprisingly few studies of this kind. Yin and Johnson [4] attempted to apply light to plants as different 'arrangements' over time but retaining the same integrated photon flux density in each case. Figure 2 shows an example of the patterns of light used. They discovered a complex set of acclimation responses where different components of photosynthesis had separate responses and where responses were not related to either the mean irradiance or the peak irradiance. Species may also respond in different ways with possible ecological relevance [5,6,7]. More complex series of light transients and discussion of thresholds with respect to short term changes in photosynthesis only can be found in [2].

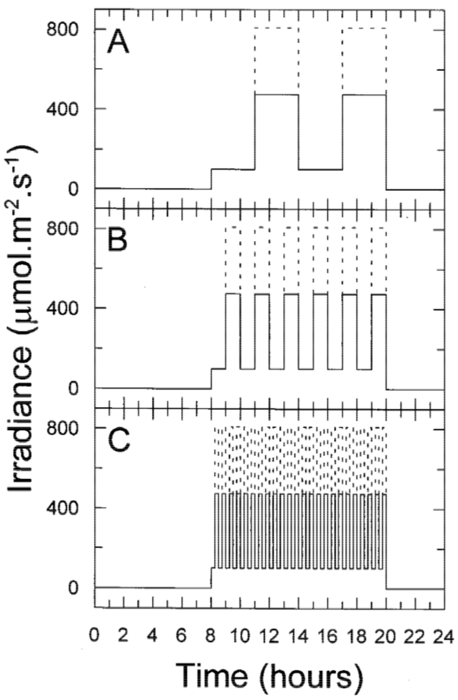


Figure 2. Fluctuating light regimes used in [4]. During the 12h photoperiod , light was switched between 100 and 475 μmol m^{-2} s^{-1} (solid lines) or between 100 to 810 μmol m^{-2} s^{-1} (dashed lines). The duration of the high and low periods was 0.25 (A), 1 (B), or 3 (C) hours with equal duration of the low light and high light. The average daytime irradiance was constant at 288 μmol m^{-2} s^{-1} for all 100/475 regimes and at 455 μmol m^{-2} s^{-1} for all 100/810 regimes.

However light in nature is much more heterogeneous and unpredictable than that used in such experiments and there are not many examples of direct observation of acclimation outside the artificial environment of a growth room.

The adaptive advantage of acclimation in nature is not questioned: a simple calculation of quantum yield and photosynthetic capacity can show this. In addition a recent study [8] noted that in a mutant of *Arabidopsis thaliana* that lacked the ability to acclimate, growth and fitness was reduced in a variable environment. When the mutant was grown in the 'steady –state' environment of a growth room there was no cost for the lack of acclimation.

The problem posed and the overall aim of the study:

Given the recent evidence showing the importance of acclimation [6] it is timely to reinvigorate our understanding of acclimation in natural and agricultural systems. The main problem in our opinion is that we don't actually know the precise pattern of light changes (and the consequential alterations in photosynthesis and signal transduction) that are needed to trigger acclimation (Figure 3).

The overall aims of this study would be firstly to develop a data driven study to examine correlations between patterns of light input and response output using appropriate datasets e,g [4]. It would also be interesting to examine interactions with knowledge of existing signal transduction systems (figure 4). Secondly to devise a model based on current knowledge of acclimation that would, for example, be able to predict the adaptive (photosynthetic)

advantage from acclimating or not acclimating to particular combinations of light sequences that mimic those found in real environments.
To achieve these aims we suggest utilizing some unpublished data e.g. from [4] and published data from the reference list below elsewhere. Where possible we will obtain unpublished data from collaborators.

Key questions:

1. Does the plant simply sense the variation alone (perhaps with a direction indicator) or is acclimation truly quantitative in nature?
2. Assuming that plants have a means of quantifying the environment, is there a threshold response or a cumulative indicator that triggers acclimation?
3. Generally plants need to be 2 – 3 days in an environment before acclimation occurs: what is the significance of this in terms of signal transduction?
4. What adaptive advantage is there to acclimation in a changing environment i.e. is there an element of 'investment risk' involved?

Figure 3. Schematic indicating the major problems to be addressed

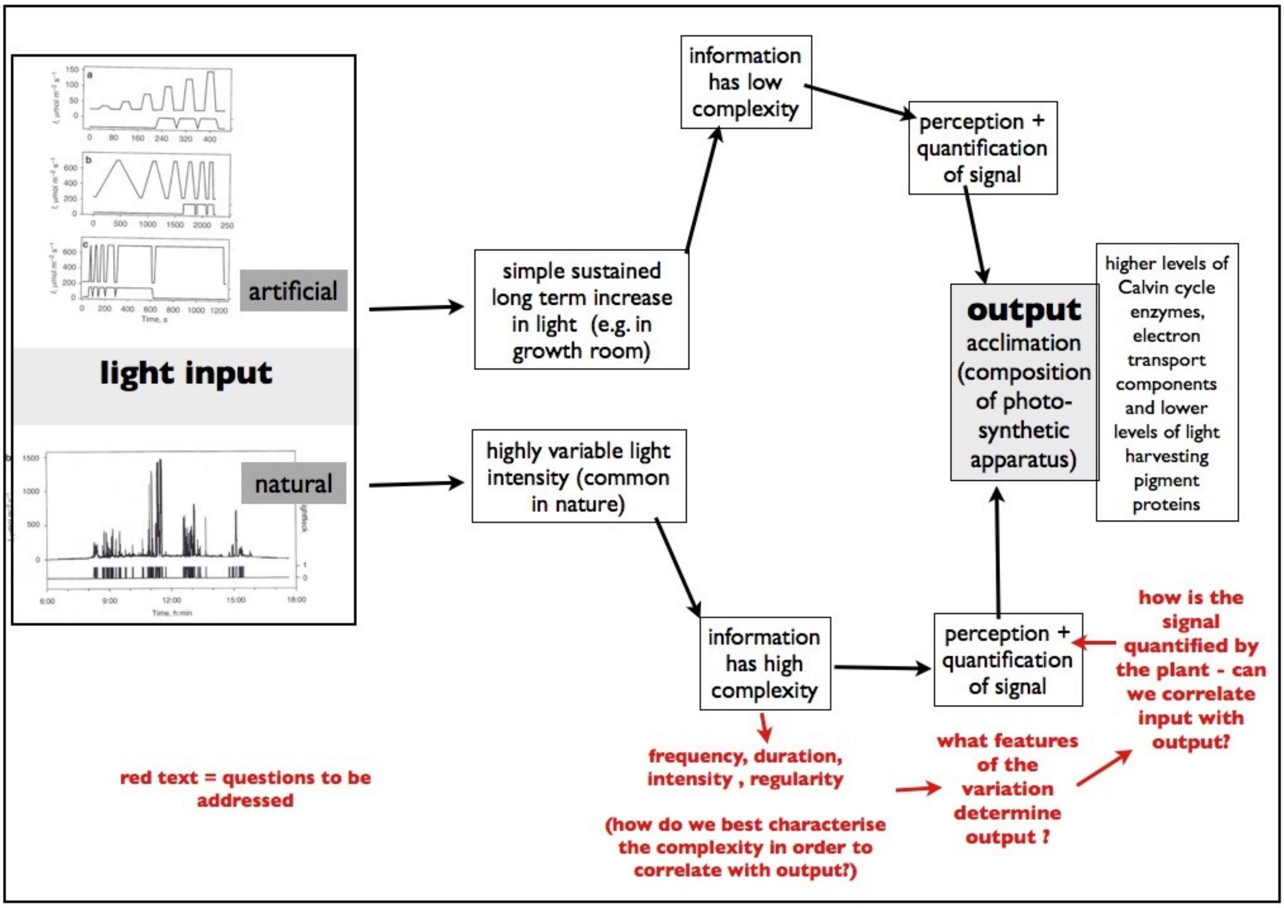
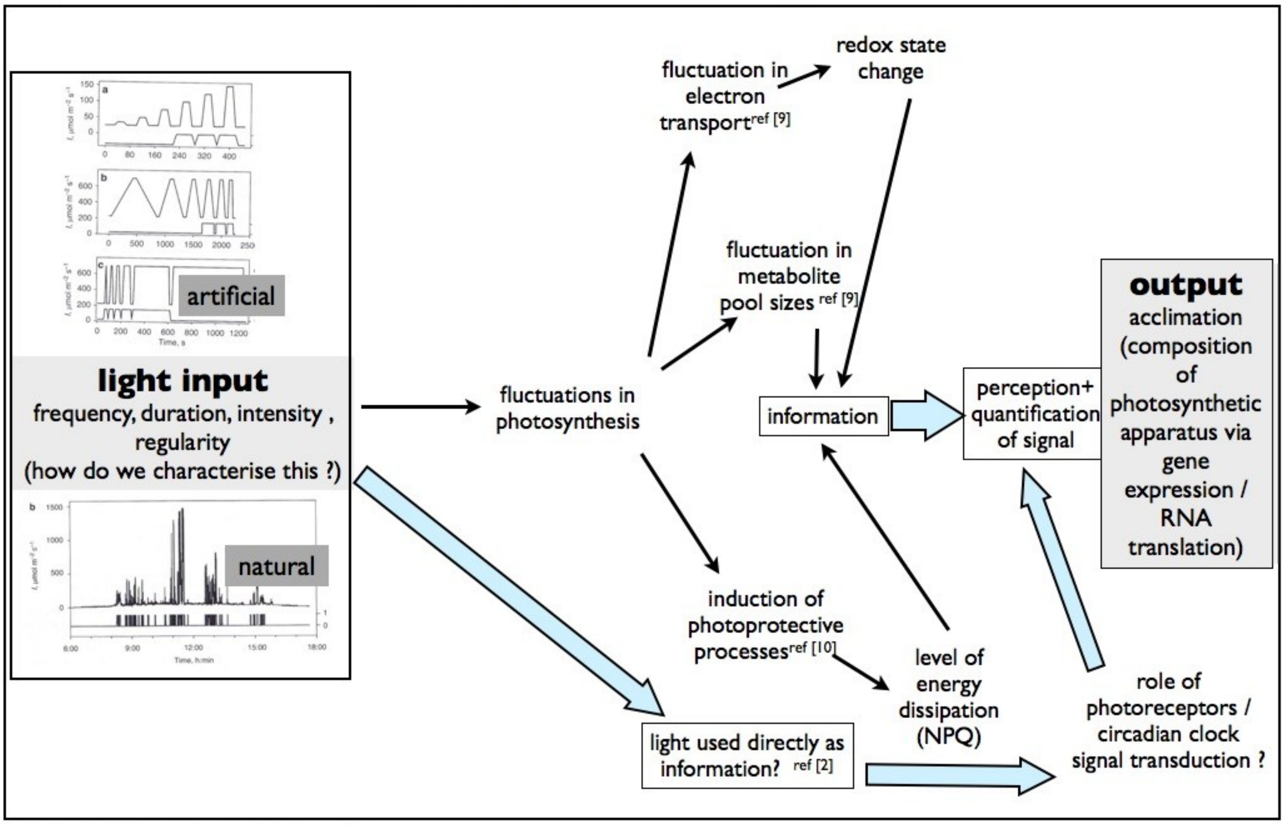


Figure 4. schematic indicating major perception / signalling processes involved in acclimation



block arrows - 'flow' of information
line arrows - metabolic change

References

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