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A shadow detector for photosynthesis efficiency

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ABSTRACT

Plants tolerate large variations in the intensity of the light environment by controlling the efficiency of solar to chemical energy conversion. To do this, plants have a mechanism to detect the intensity, duration, and change in light as they experience moving shadows, flickering light, and cloud cover. Sugars are the primary products of CO_2 fixation, a metabolic pathway that is rate limited by this solar energy conversion. We propose that sugar is a signal encoding information about the intensity, duration and change in the light environment. We previously showed that the Arabidopsis heterotrimeric G protein complex including its receptor-like Regulator of G signaling protein, AtRGS1, detects both the concentration and the exposure time of sugars (Fu et al., 2014. Cell 156: 1084–1095). This unique property, designated dose-duration reciprocity, is a behavior that emerges from the system architecture / system motif. Here, we show that another property of the signaling system is to detect large changes in light while at the same time, filtering types of fluctuation in light that do not affect photosynthesis efficiency. When AtRGS1 is genetically ablated, photosynthesis efficiency is reduced in a changing- but not a constant-light environment. Mathematical modeling revealed that information about changes in the light environment is encoded in the amount of free AtRGS1 that becomes compartmentalized following stimulation. We propose that this property determines when to adjust photosynthetic efficiency in an environment where light intensity changes abruptly caused by moving shadows on top of a background of light changing gradually from sun rise to sun set and fluctuating light such as that caused by fluttering leaves.

1. Introduction

Cells detect different chemical stimuli through binding the corresponding signaling molecule to specific receptors that consequently trigger an appropriate response. In many situations, the concentration of these signaling molecules is not static but changes over time. Therefore, cells not only need to act as threshold detectors, but must also be able to interpret or filter temporal variations in the signal. Understanding the control mechanisms that allow cells to respond to changing environmental conditions is a fundamental problem in cell biology.

Two examples demonstrate the importance of time-dependent signaling. The first example pertains to killer T-cell activation by antigen presentation. T-cells must tolerate slowly-changing levels of antigens while still remaining competent to become activated in response to acute changes in antigen presentation. This is a critical decision because commitment to activate is both energetically costly and precarious to healthy cells. To accomplish this, a change detector for T-cell activation was proposed by Kim and Lee (2011) by which T cells compare instantaneous changes in signals to long-term steady-state levels. The second example pertains to plant cells deciding how to allocate newly-fixed carbon, mostly as sugars. Sugar levels change dramatically between the day and night (Deuschle et al., 2006) and sources of and sinks for sugars also change over time independently of the changes over the diel cycle. Recently, we proposed a mechanism called Dose-Duration Reciprocity to explain how plant cells are able to generate a maximal response to both low-sustained and high-transient glucose levels (Fu et al., 2014).

Here, we present a third example that demonstrates how plants are able to respond to rapid changes in both signal frequency and amplitude on top of slow variations in baseline levels. Plants are sessile and unable to escape their environment, therefore they evolved cellular and chemical control mechanisms to cope with the variability of sunlight impinging on the plant. The time scales of this variability can range from sub-seconds to hours. Moving clouds reduce light to

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different levels and for different times, shadows produce large changes in light over minutes, and moving leaves produce flickering light in a time scale of sub-seconds to seconds. These types of fluctuations occur in the presence of large changes in light caused by the Earth's daily rotation. In other words, the light signal fluctuates on top of a periodically changing baseline. Therefore, a simple threshold detector is not sufficient for plants to efficiently utilize sunlight; rather additional control mechanisms that allow plants to interpret changing environmental conditions are required.

Without the ability to respond to temporal changes in light, unquenched solar energy would destroy the photosynthetic antenna and potentially kill the entire leaf. On the other hand, not maximizing photosynthesis efficiency reduces competitiveness with potential lethal consequences when neighbors consume the limited light resource. The key question then is how photosynthetic cells detect light change and maximize photosynthetic efficiency accordingly while at the same time guard against photobleaching in a light environment that is unpredictable in duration and intensity.

The identity of the control signals is not known but it is logical to assume that they are products of the light-dependent and dark processes. The immediate products of the light reaction are NADPH, ATP, O_2, and protons, which are pumped across the thylakoid membrane of the chloroplast to create a steep pH gradient between the stroma and thylakoid space (lumen). CO_2 fixation occurs in the stromal space and is strictly dependent on pH and ATP (Werdan et al., 1975). The immediate product of CO_2 fixation is glycerate-3-phosphate which requires ATP and NADPH for final conversion to hexoses, including glucose, thus glucose is rate-limited by the light reactions.

The AtRGS1/heterotrimeric G protein complex is one of three well-studied detectors of glucose in plants (Chen et al., 2003, 2006; K. Booker et al., 2010; Chen and Jones, 2004; Urano et al., 2012b). AtRGS1 is the prototype 7-transmembrane (7TM) Regulator of G Signaling (RGS) family of GTPase-accelerating proteins (Chen et al., 2003). We constructed a mathematical model of the G protein signaling pathway in plant cells that enables both the concentration and duration of glucose to control cell behavior. The model is shown in Fig. 1A. In this model, the AtRGS1/G protein cycle is not described by a simple two-state system, rather the model describes frequent oscillation between an inactive set of intermediates (left cycle in Fig. 1A) and an active set of intermediates (right cycle in Fig. 1A). In contrast to animal G proteins, the Gα subunit of the plant heterotrimeric G protein complex spontaneously exchanges bound GDP for GTP (Johnston et al., 2007; Urano et al., 2012a). GTP is not limiting in cells, therefore control occurs by holding the G protein complex in its GDP-bound, inactive state. The Gα binding is in equilibrium between the RGS and Gβγ sites, but D-glucose shifts the equilibrium toward the RGS site and releases Gβγ. AtRGS1 accelerates GTP hydrolysis and interacts with different G protein complex intermediates at the plasma membrane. Thus, removal of AtRGS1 from the plasma membrane allows the G protein complex to move from the inactive cycle to the active cycle. This occurs by AtRGS1 endocytosis (the central part of Fig. 1A). Previously, we found that to appropriately respond to glucose signals of varying strength and duration required two kinases with distinct biochemical properties (Fu et al., 2014). The first kinase has fast activation kinetics used for pulses of high concentrations of glucose. The second kinase has slow kinetics used for long periods of low concentrations of glucose. Both kinases are members of the WITH NO LYSINE (WNK) kinase family (Urano et al., 2012b); kinase 1 is encoded by the *WNK8* and *WNK10* genes (x_{15}) and kinase 2 is encoded by the *WNK1* gene (x_{14}).

Here, we show that under conditions of fluctuating light the photosynthesis efficiency of Arabidopsis depends on AtRGS1. Therefore, in addition to dose and duration, the AtRGS1/G protein system detects other temporal properties of natural sunlight. In particular, we use mathematical modeling to demonstrate that the AtRGS1 system has the ability to detect the temporal boundaries between changes in sunlight intensity through free AtRGS1, Gα^{GTP}, and Gβγ while filtering noise and remembering the immediate past signaling history. We propose a system motif that encodes the requisite properties of change detector, filter, and memory.

In the following sections, we show that detection of light fluctuations is a property of the AtRGS1/G signaling system and is a form of adaptation behavior. Disruption of this system abrogates the ability of plant cells to regulate the efficiency of photosynthesis in leaf cells. By assuming a direct positive correlation between light intensity/duration and glucose, the signaling system has the emergent property of detecting changes in light intensity and duration such as occurs with shadows passing across the leaf. Interestingly, this property does not require the WNK kinases previously shown to be important for dose-duration reciprocity whereas system memory does. The primary mechanism for this emergent property is the formation and dissociation of AtRGS1:G$\alpha^{GTP}\beta\gamma$ and AtRGS1:Gα^{GTP}. The amounts of free AtRGS1, Gα^{GTP}, and Gβγ are the major constituent of the change detector, and the amount of free AtRGS1 is also the major constituent of the filter. Finally, we speculate that this change detector informs the plant of fluctuations in sunlight intensity used to make the appropriate adjustments in photosynthesis efficiency. This is important in locations such as canopy understory where neighboring plants temporarily shade each other.

2. The emergent property: change detection

Considerable evidence supports AtRGS1 as a component of a glucose-sensing pathway (Ullah et al., 2001; Grigston et al., 2008; K.S. Booker et al., 2010; Urano et al., 2012a), however, because many grasses lack homologous 7TM-RGS proteins yet retain a functional heterotrimeric G protein complex (Urano et al., 2012a, 2015), the role of a 7TM-RGS protein in glucose sensing must be peripheral such as an add-on component that provides a unique function. In this sense, AtRGS1 is a modulator. Therefore, we hypothesized that AtRGS1 imparts some glucose sensing property needed for non-grass plants, specifically the ability to compete in fluctuating light such as within a canopy. Grasses are unable to compete well with other plant species for access to light and are not successful on forest floors. Biomes where grasses are found are open, typified by the savannahs of the pampas fields in Argentina, the grassland prairies of the Midwest US, and wild rice marshes throughout the world. These biomes do not have forest canopies and thus are not heavily subjected to fluctuation by shadows. Plants that contain 7TM RGS proteins grow in communities where they must compete with other species for light access with maximum efficiency. This suggests that AtRGS1 improves plant fitness in fluctuating light environments. We expect that RGS proteins extracts important features and information from the light pattern that provides plants using RGS proteins with a property that affords a competitive advantage over the grasses which lack RGS proteins.

We assumed that this property involved glucose produced by photosynthesis therefore we compared photosynthesis parameters in plants having or lacking a functional AtRGS1 protein. We tested this idea by subjecting 5-week-old plants to stable and changing light conditions (Fig. 1B) while simultaneously determining photosystem II (PS II) efficiency, nonphotochemical quenching (NPQ, total ability to dissipate energy), the reversible component of NPQ (qE), and the irreversible component of NPQ or photodamage (qI). As shown in Fig. 1C–F, *rgs1* null mutants behaved similarly to wild type (WT) under flat day conditions (lights on → lights off, Fig. 1B). However, under varying light, the *rgs1* mutants were less efficient in photosystem II. In the first condition, the light environment approximated a sinusoidal pattern using small steps in order to mimic the natural environment of light slowly increased from the experimental dawn time point up to its maximum then decreased to the experimental dusk time point. The second changing light environment was like the first except with pulses of light added. The difference in photosynthesis efficiency between wild type and *rgs1* mutants was observed in all 7 biological replicates and to similar degree in most of the replicates. *rgs1* mutants had a decreased PS II efficiency (Fig. 1C) due to increased NPQ (Fig. 1D). The regulated and reversible qE

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