

Minireview

Interactions between light and carbon signaling pathways in *Arabidopsis*

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Abstract

Two major signals perceived by plants are light and the source of carbon. A new report has examined the interactions between the signaling pathways from these two stimuli on a genome-wide scale in the model plant *Arabidopsis thaliana*.

When a seed germinates under the soil in darkness, the initial growth and development of the seedling is fueled by mobilization of the carbon reserves, which are stored in the cotyledons in dicotyledonous plants (dicots) and the endosperm in monocotyledonous plants (monocots). The dark-grown (etiolated) seedling is then competent to perceive light signals. When the etiolated seedling emerges from the soil, light immediately triggers changes in its growth and development and promotes the dramatic transition from feeding on chemical compounds (heterotrophy) to synthesizing food using light energy (autotrophy). Carbon compounds such as sucrose that are made during photosynthesis in seedlings are transported from the photosynthetic tissues to the rest of the seedling, where they are converted to starch for storage.

As the metabolic requirements and developmental needs of a plant are so different in light and darkness, or in the presence and absence of a supply of carbon, it is not surprising to see complex interactions between the two signals in regulating gene expression. Certain photosynthetic genes (such as the *cab* genes, which encode the light-harvesting chlorophyll a/b binding proteins) are induced by light but repressed by carbon, whereas other genes are induced by both signals. Until now, however, no-one has attempted a systematic analysis to explore the complexity of these interactions at a genome-wide scale; nor have models been proposed to describe these interactions.

The Coruzzi laboratory has pioneered the systematic analysis of interactions between light and carbon signaling pathways in the model plant *Arabidopsis thaliana*. Using the genes *ASN1* and *ASN2* (encoding asparagine synthetases), and *GLN2* (encoding a glutamine synthetase), they found that although carbon regulates the expression of *ASN1* and *GLN2* in etiolated seedlings, this regulation can be overridden by light [1]. Conversely, in light-grown plants, carbon supplants light as the major regulator of *GLN2* and *ASN2*. These regulatory interactions appear to reflect the different roles of glutamine and asparagine in light- and dark-grown plants.

In an article recently published in *Genome Biology* [2], Coruzzi and colleagues have extended their investigations into interactions between light and carbon signaling to many more genes. Two-week-old *Arabidopsis* plants were left untreated or treated with light and carbon (sucrose), giving four conditions denoted '-C-L' (control without carbon or light), '-C+L' (light only), '+C-L' (carbon only), and '+C+L' (both); RNA samples from each condition were analyzed using Affymetrix chips containing 8,000 genes (about 30% of the entire genome). Expression profiles obtained from the experimental samples were compared with that of the -C-L sample in order to measure the effect of the two signal inputs for a total of about 2,000 genes for which complete microarray data were obtained.

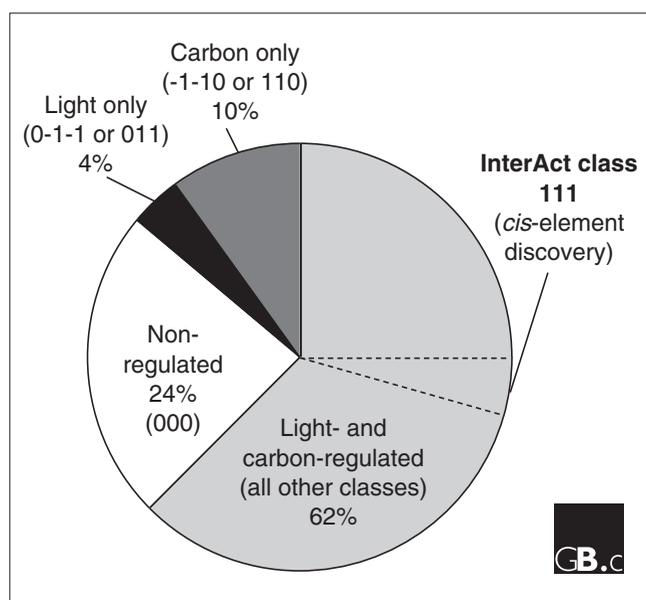


Figure 1
Dissecting light and carbon signaling interactions in *Arabidopsis thaliana*. From microarray data derived from carbon- and light-treated *Arabidopsis* plants, the Coruzzi group [2] defined InterAct classes as sets of genes that have similar expression profiles in response to light and/or a carbon source. The proportions of genes (for which there were sufficient data) that were regulated in each possible way by carbon and light are shown. One InterAct class (111), in which both carbon and light have the same effect whether separately or in combination, was used to define putative DNA *cis* elements involved in responding to light or carbon.

To simplify and understand the patterns observed, the authors [2] developed analytical tools to sort and classify differences in gene expression under different conditions into

discrete groups, named 'InterAct classes'. By assigning a numerical value to the effect observed, the classification reflects the individual and combined effects that carbon and light have on particular genes. The effects are listed in the order C, C+L, L, and negative values were used to show a repressive response to a given signal; the values given reflect only whether one response is higher than another, not the amount by which it is increased. For example, a gene induced by either carbon or light (independently), and with an additive effect in the presence of both signals, was placed in class 121 (1 for induction with carbon alone, 2 for greater induction with carbon and light, and 1 for induction with light alone). Another gene that responded only when carbon and light are present was assigned to InterAct class 010. This elegant classification of gene-expression patterns obtained with combinations of two different signals effectively reduces the complexity observed in microarray data while maintaining its qualitative character. Consequently, Thum *et al.* [2] found genes regulated by neither signal (InterAct class 000) and genes that responded exclusively to only one input (classes 110, -1-10, 011, and 0-1-1; see Figure 1).

The authors [2] focused their attention on the 62% of the 2,000 genes (see Figure 1) that showed complex expression patterns in response to both signals. Detailed analysis of the different InterAct classes led the authors to propose three different models for carbon and light interactions (Table 1; see also Figure 1 in [2]). Carbon and light signals can regulate gene expression either independently (model 1: InterAct class 121 is a good example), in an exclusively dependent manner, whereby a change in expression is observed only if both signals are present (model 2, classes 010 and 0-10), or in a combined dependent and independent manner (model 3; see Table 1 for some of the numerous combinations found in this model).

Table 1

Assignment of InterAct classes and models

Treatments			Light-carbon interactions			
+C/-L	+C/+L	-C/+L	InterAct class	Interaction	Model	Examples of other classes in the same model
No change (0x)	Induced (3x)	Induced (3x)	011	None; responds only to light	None	110, -1-10, 0-1-1
Induced (5x)	Induced (10x)	Induced (5x)	121	Inductive	Independent (model 1)	Repressive (such as -1-2-1); antagonistic (such as -10-1)
No change (0x)	Induced (3x)	No change (0x)	010	Synergistic	Dependent (model 2)	010 (also synergistic)
Induced (5x)	Induced (5x)	Induced (5x)	111	Equal effect (whether separately or together)	Independent and dependent (model 3)	C dominates (such as 221); L dominates (such as 122); suppressed (such as 210); Enhanced (such as -1-20)

For simplicity, the values for each condition that make up the InterAct classes reflect only whether one response is higher than another, not the amount by which it is increased with respect to the untreated (-C,-L) sample. For example, the threefold induction in the first row and the fivefold induction in the second row are both counted as 1 and the tenfold induction as 2. See text for further details. Modified from Thum *et al.* [2].

Recognizing that this analysis could potentially give important insights, Coruzzi and colleagues [2] then used the functional classification of the Munich Information Center for Protein Sequences (MIPS) [3,4] to identify functional categories of genes underpinning metabolic pathways likely to be regulated by carbon and/or light signaling. They found that genes in the categories 'carbon-containing-compound/carbohydrate metabolism', 'cell wall' and 'electron transport' are overrepresented in InterAct class 111 (and thus are likely to be regulated by either carbon or light), whereas the functional categories 'transcription', 'cellular communication/signal transduction' and 'cell cycle and DNA processing' are overrepresented within InterAct class 000 and thus, as a whole, are less likely to be regulated by carbon or light signaling pathways.

Genes with similar regulation patterns (that is, genes that are in the same InterAct class) are likely to share common *cis* elements that mediate their expression. To investigate whether this is the case, the authors [2] analyzed a subset of genes involved in similar metabolic processes within a single InterAct class (111) in which both carbon and light have the same effect, whether separately or in combination. They were able to identify DNA sequence elements capable of responding to either one of the signals, putative 'light-or-carbon responsive' elements. At each step of their work, the authors provided strong indications of confidence in their approach. It is clear that well-characterized genes indeed fall into the 'correct' categories according to their known expression profiles. Furthermore, known light-responsive *cis*-acting motifs are found among the newly described putative light-or-carbon-responsive elements, including GT-1 binding sites, G-boxes, H-boxes and RE1 elements (see Table 7 in Thum *et al.* [2]).

The systems-biology approach described by the Coruzzi group [2] can potentially be applied to investigating interactions of any other pair of signals that mutually modulate a plant developmental process. For example, it is known that responses to pathogen invasion are dependent on light [5], and ethylene and jasmonic-acid signaling pathways act synergistically as well as antagonistically in regulating gene expression [6]. Detailed descriptions and modeling of these interactions using the methods provided in this study [2] will eventually lead to a more complete understanding of how plant signaling systems operate.

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