A global expression analysis of the shade avoidance response in Arabidopsis thaliana

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Motivation

Crop productivity depends on the acquisition of resources and their distribution within the plant to harvestable components. Resource allocation is highly plastic, and can be regulated by many environmental factors. Temperature and water availability can exert a profound influence on plant shape, affecting overall size as well as the number and size of different organs. However, the major determinant of plant architecture in the field is the response of the plant to signals from the light environment. Plants growing in close proximity exhibit the shade avoidance syndrome in response to reflected far-red (FR) radiation from neighbours. Shade avoidance results in elongated internodes, reduced branching, weaker leaf development, accelerated flowering and diminished fruit set. Shade avoidance is a strategy of major adaptive significance to plants in natural communities, particularly to the angiosperms from which most of the crop species have been developed. However, the re-allocation of resources to competitive growth reduces their availability for storage and reproduction, leading to diminished crop productivity. To develop effective strategies that increase crop yields under high density growth conditions, a molecular description of the shade avoidance response is an important initial step. To this end, a global approach was used to highlight expression changes induced by FR-rich light in Arabidopsis, taking advantage of all the bioinformatics tools developed for this model organism.

Methods

Early and late events of the shade avoidance response in Arabidopsis were investigated by means of Affymetrix Arabidopsis Genome GeneChip array (ATH1) analyses on young seedlings exposed to low red (R)/FR light for short (1, 4 hours) and prolonged (1, 4 days) times. After identification of statistically significant low R/FR-responsive genes (one-way ANOVA, Student's t-test with FDR= 0.05), Genevestigator meta-profile analyses was used to study expression patterns across different ontology categories. Functional classification of low R/FR regulated genes was carried out by means of The Arabidopsis Information Resource (TAIR), a comprehensive database of genetic, molecular and bioinformatics data for this plant.

Moreover, we analysed groups of co-expressed genes to identify shared regulatory motifs. To this aim, we implemented Perl scripts to analyse putative promoter regions of low R/FR-regulated genes and identify over-represented promoter elements (http://pegaso1.bio.uniroma1.it/msblab/PLACE.php). Known plant promoter elements and their annotation were downloaded from the PLACE database. For each set of n co-expressed genes, we compared the number of occurrences for each motif in PLACE against the average number of occurrences within 1,000 randomly generated sets of n promoters. The one-tailed p-value for each motif is based on the Z-score of the difference of the actual word count of the promoter set (C_{true}) minus the mean count from the 1,000 surrogates (C_{rand}) relative to the SD from the 1,000 surrogates (SD_{rand}) [i.e., $Z=(C_{true} - C_{rand})/SD_{rand}$].

Results

The transcriptome analysis of Arabidopsis seedlings briefly exposed to low R/FR revealed a rapid induction of a large number of genes functionally involved in light and hormone signalling. Strikingly, auxin, gibberellin and brassinosteroid pathways are up-regulated whereas cytokinin signalling is down-regulated. These changes in hormone pathways are consistent with the enhanced elongation growth of stem-like organs as well as with the reduced proliferative activity of leaf-like organs.

Remarkably, promoter analyses showed an evident over-representation for light and hormone signalling related regulatory motifs, giving a further confirmation on the prominent role of these pathways in shade avoidance responses. Interestingly, transcriptome analysis of seedlings exposed to prolonged low R/FR revealed that gene expression changes in hormone and light pathways are transient, implying that persistency of the signal results in plant acclimation. Taken together, our data underline the marked difference between the early and delayed events of the shade avoidance response. The first ones are characterised by a strong induction of genes encoding regulatory molecules which eventually trigger the developmental changes caused by low R/FR exposure, whereas the second ones are characterised by broader and more complex changes in gene expression aimed to sustain the growth of the plant even in adverse light conditions.

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