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## Research paper

# Genetic variation in transcription factors and photosynthesis light-reaction genes regulates photosynthetic traits

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Transcription factors (TFs) play crucial roles in regulating the production of the components required for photosynthesis; elucidating the mechanisms by which underlying genetic variation in TFs affects complex photosynthesis-related traits may improve our understanding of photosynthesis and identify ways to improve photosynthetic efficiency. Promoter analysis of 96 nuclear-encoded *Populus tomentosa* Carr. genes within this pathway revealed 47 motifs responsive to light, stress, hormones and organ-specific regulation, as well as 86 TFs that might bind these motifs. Using phenotype–genotype associations, we identified 244 single-nucleotide polymorphisms (SNPs) within 105 genes associated with 12 photosynthesis-related traits. Most (30.33%) of these SNPs were located in intronic regions and these SNPs explained 18.66% of the mean phenotypic variation in the photosynthesis-related traits. Additionally, expression quantitative trait loci (eQTL) mapping identified 216 eQTLs associated with 110 eGenes (genes regulated by eQTLs), explaining 14.12% of the variability of gene expression. The lead SNPs of 12.04% of the eQTLs also contributed to phenotypic variation. Among these, a SNP in *zf-Dof 5.6* (G120\_9287) affected photosynthesis by modulating the expression of a sub-regulatory network of eight other TFs, which in turn regulate 55 photosynthesis-related genes. Furthermore, epistasis analysis identified a large interacting network representing 732 SNP–SNP pairs, of which 354 were photosynthesis gene–TF pairs, emphasizing the important roles of TFs in affecting photosynthesis-related traits. We combined eQTL and epistasis analysis and found 32 TFs harboring eQTLs being epistatic to their targets (identified by eQTL analysis), of which 15 TFs were also associated with photosynthesis traits. We therefore constructed a schematic model of TFs involved in regulating the photosynthetic light reaction pathway. Taken together, our results provide insight into the genetic regulation of photosynthesis, and may drive progress in the marker-assisted selection of desirable *P. tomentosa* genotypes with more efficient photosynthesis.

**Keywords:** association genetics, epistasis, eQTL, photoinhibition, photosynthetic light reaction, *P. tomentosa*, regulatory network, transcription factor.

## Introduction

Improving the efficiency of photosynthesis, the complex process in which light energy is converted to chemical energy, has the potential to increase crop yields and prevent food shortages. For woody species, improved photosynthesis has the potential to increase carbon fixation and improve the production of biomaterials such as

wood and fiber. However, the efficiency of photosynthetic reactions can only be genetically improved by a coordinated, system-wide approach targeting a variety of steps along the process (Blankenship 2013). The first stage of photosynthesis, the light-dependent reactions providing the reducing power for carbon fixation, takes place mainly on the chloroplast thylakoid membranes.