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ORIGINAL ARTICLE

Allelic variation in *PtoPsbW* associated with photosynthesis, growth, and wood properties in *Populus tomentosa*

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Abstract Photosynthesis is one of the most important reactions on earth. PsbW, a nuclear-encoded subunit of photosystem II (PSII), stabilizes PSII structure and plays an important role in photosynthesis. Here, we used candidate gene-based linkage disequilibrium (LD) mapping to detect significant associations between allelic variations of *PtoPsbW* and traits related to photosynthesis, growth, and wood properties in *Populus tomentosa*. *PtoPsbW* showed the highest expression in leaves and it increased during the development of these leaves, suggesting that *PtoPsbW* may play an important role in plant growth and development. Analysis of nucleotide diversity and LD revealed that *PtoPsbW* has low single-nucleotide polymorphism (SNP) diversity ($\pi_{tot} = 0.0048$ and $\theta_w = 0.0050$) and relatively low average value of LD (0.1500), indicating that *PtoPsbW* is conserved due to its indispensable function. Using single-SNP associations in an association population of 435 individuals, we identified five significant associations at the threshold of $P \leq 0.05$, explaining 3.28–15.98 % of the phenotypic variation. Haplotype-based association analyses indicated that 13 haplotypes ($P \leq 0.05$) from six blocks were associated with photosynthesis, growth, and wood properties. Our work shows that identifying allelic variation and LD can help to decipher the genetic basis of photosynthesis and could potentially be applied for molecular marker-assisted selection in *Populus*.

Keywords Photosystem · Photosynthesis · PsbW protein · Single-nucleotide polymorphisms · Haplotype-based association analyses · Linkage disequilibrium · *Populus tomentosa*

Introduction

Trees cover 82 % of terrestrial ecosystems and have important roles as renewable sources for biofuels, biomaterials and in regulating climate (Neale and Kremer 2011). More than 90 % of crop biomass derives from photosynthetic products (Makino 2011). Photosynthesis comprises a complex series of reactions and involves many interacting genes. Analyzing photosynthetic-related genes at the molecular level may provide new perspectives on how to improve photosynthesis. However, few studies have focused on dissecting the mechanism of photosynthesis via examining the single-nucleotide diversity of photosynthesis-related genes and association analysis.

Nuclear-encoded subunit of photosystem II (PSII) is a large cofactor–protein supercomplex containing more than 40 proteins encoded by both plastid and nuclear DNA and many cofactors, which carries out the first reaction of photosynthesis, one of the most important reactions on Earth (Barber 2005, 2006). The nuclear-encoded PsbW subunit of PSII plays an important role in stabilizing the supramolecular organization of PSII in higher plants; for example,

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