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ARTICLE ADDENDUM

The role of arabidopsis WDR protein in plant growth and defense strategies

Huey-wen Chuang, Ji-Huan Feng, and Yung-Lin Feng

Department of Bioagricultural Sciences, National Chiayi University, Chiayi, Taiwan

ABSTRACT

Evidence indicates that the mechanisms controlling photosynthesis efficiency also regulate plant response to biotic and abiotic stress. Light-induced cell death is genetically maintained for the control of innate immunity. In a recent study we showed that the expression of *AtWDR26* was induced by light, multiple plant hormones, and abiotic stress; increased *AtWDR26* strongly upregulated gene groups related to chloroplast metabolism, disease resistance, and abiotic stress tolerance. Gain- and loss-of-function analyses in transgenic plants demonstrated the involvement of *AtWDR26* in signaling pathways; these controls were osmotic as well as salt stress tolerance. More detailed transcriptome evidence suggested that *AtWDR26* was a powerful inducer of gene expression associated with chloroplast metabolism. This included the electron transport chain of the photosystem, carbohydrate synthesis, and enzymatic activity involved in photorespiration. Moreover, genes in auxin synthesis (and perception) constituted a significant portion of those that were upregulated. Gene expression involved in disease resistance, control of cell wall flexibility, Zn uptake, and AP2/ERF transcription factors was also be upregulated. We concluded that *AtWDR26* is one component in the regulatory network between light-regulated plant growth and the adaptation response to disease resistance and abiotic stress. Auxin signal acts downstream for *AtWDR26* regulation and the adaptation response to biotic and abiotic stress: this occurs through modulating cell wall flexibility, Zn homeostasis, and controlling stress-related transcription factors.

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Light is the most essential environmental factor for plant growth and development. Plant cells have evolved a highly responsive and flexible system to cope with excess excitation energy, generated by high light stress. Efficient acclimation to high light growth conditions is relied on a proper communication between chloroplast signals and nucleus gene expression. Accumulating evidence suggests the involvement of cellular pathways, including redox signals derived from the electron transport chain, carbohydrate metabolism, and phytohormones for chloroplast retrograde signaling.[1] In a previous study, we characterized the function of the *Arabidopsis* WDR gene, *AtWDR26*.[2] The homolog of *AtWDR26* plays a role in the cellular pathway of H_2O_2-induced cell death.[3] The *AtWDR26* transcript was regulated by light and the phenotypes of transgenic seedling overexpressing *AtWDR26* and T-DNA knockout lines exhibited changes in light-regulated seed germination and seedling growth.[2] More evidence indicates that the function of WDR family proteins act as scaffolding for diverse cellular pathways.[4] The 3 largest groups of upregulated genes in transgenic seedlings overexpressing *AtWDR26* are gene groups for metabolism, stress response, and transcription regulation.[2] A detailed analysis of the *AtWDR26*-induced transcriptome revealed a large number of upregulated genes for chloroplast function, including photochemical reaction, carbohydrate synthesis, and photorespiration enzymes; moreover, genes correlated with sugar metabolism constituted the largest portion in this gene group (Fig. 1A). Photochemical reactions and peroxisome-associated reactions play important roles in high light acclimation.[5] Sugar metabolism is essential to plant cell acclimation to excess light energy.[6] Several phytohormone signals are associated with the regulation of chloroplast retrograde signaling; this includes salicylic acid (SA), abscisic acid (ABA), and jasmonic acid (JA) in the chloroplast retrograde system.[7] However, overexpression of *AtWDR26* can significantly upregulate genes involved in auxin synthesis and perception (Fig. 1B). It has been reported that carbohydrate metabolism can regulate auxin levels via the PHYTOCHROME-INTERACTING FACTOR (PIF) proteins in *Arabidopsis*.[8] Thus, it is plausible that the increased auxin signal in transgenic plants overexpressing *AtWDR26* could be the result of increased carbohydrate metabolism. More evidence for the role of auxin signaling in *AtWDR26*-regulated transcription showed increased gene expression in transgenic plants. These are genes involved in cell wall flexibility, which constituted a large portion of upregulated genes (Fig. 1C). Auxin is an important hormone in cell growth regulation that works through the modulation of cell wall flexibility.[9] Cell wall metabolism is closely correlated with the acclimation response to abiotic stress.[10] Overexpression of *AtWDR26* also upregulated genes in the control of Zn homeostasis (Fig. 1D), which is an important constituent of superoxide dismutase (SOD) functioning for the removal of oxidative stress derived from the electron transport chain in the chloroplast.[11] It is reported that exogenous auxin increases CuZn SOD levels in the tomato.[12] Auxin also plays a protective role

CONTACT Huey-wen Chuang hwchuang@mail.ncyu.edu.tw Department of Bioagricultural Sciences, National Chiayi University, Chiayi, Taiwan
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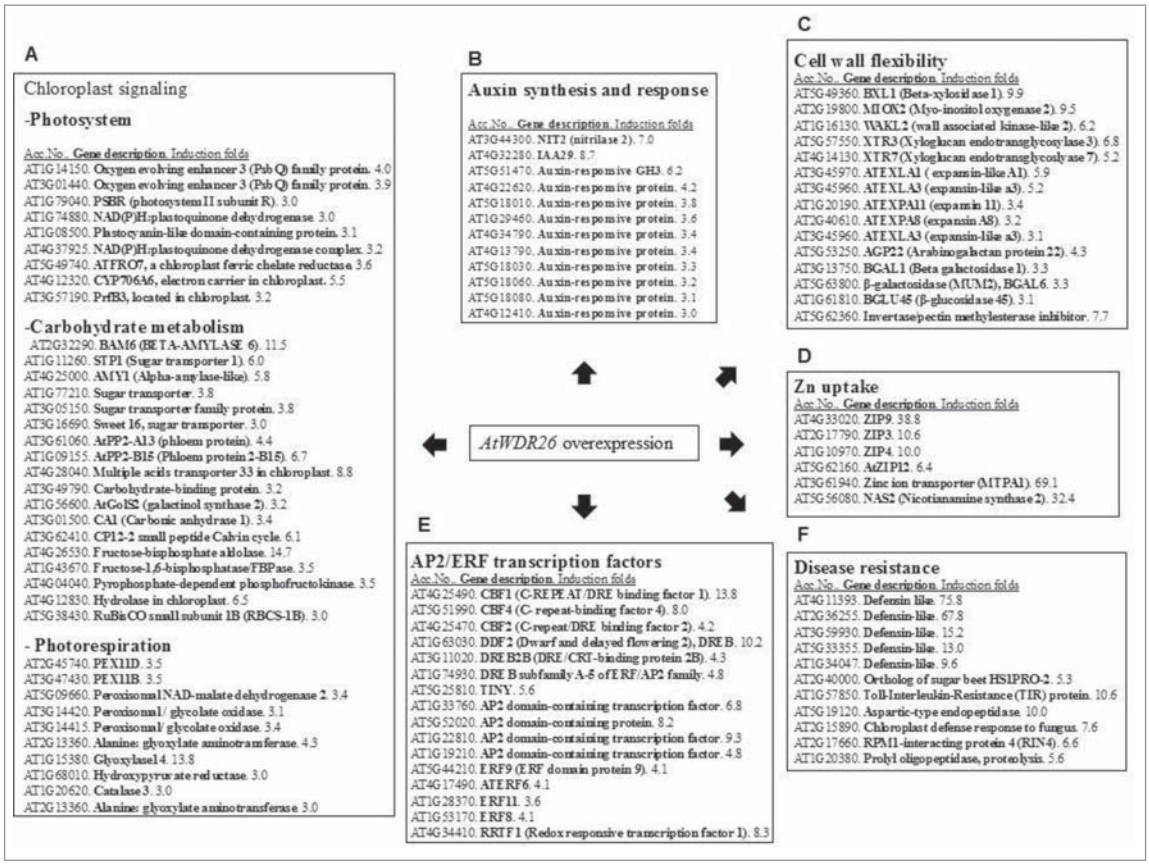

Figure 1. Selective upregulated gene groups in the transcriptome overexpressing *AtWDR26*. Transcriptome of transgenic *Arabidopsis* seedlings overexpressing *AtWDR26* was analyzed by a DNA microarray. Upregulated genes associated with chloroplast signaling (A), auxin signaling (B), cell wall flexibility (C), Zn uptake (D), transcription factors of AP2/ERF family (E), and disease resistance (upregulation levels > 5-fold) (F).

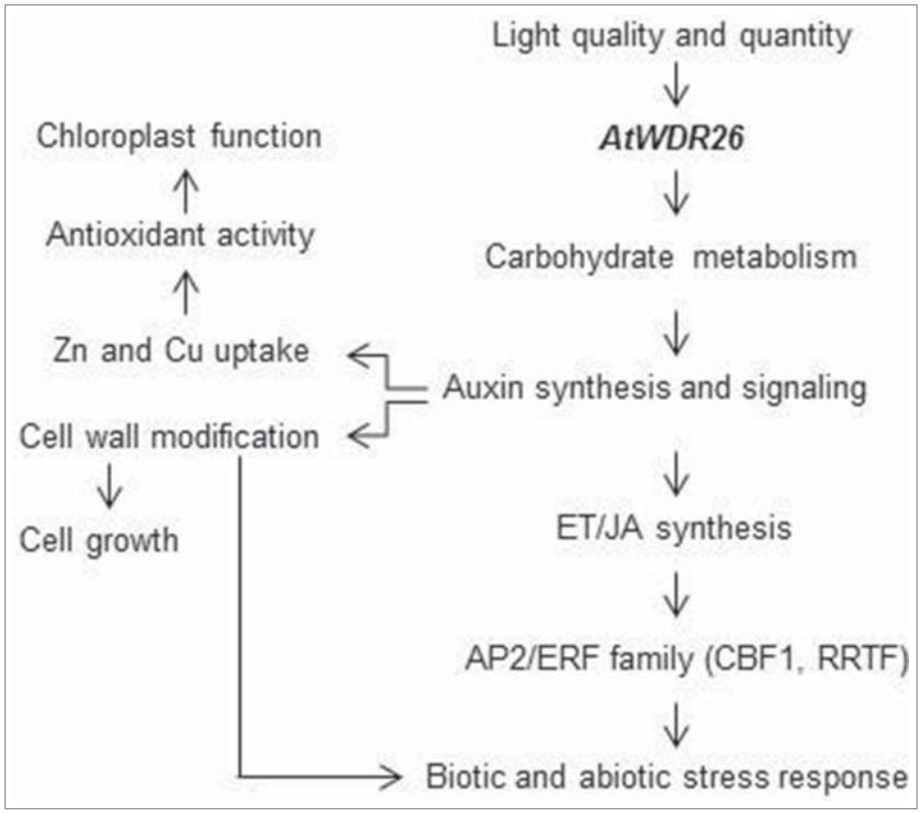

Figure 2. Model for *AtWDR26s* role in plant growth and defense response. *AtWDR26* is one component in the signaling pathway controlling light-regulated growth and development. *AtWDR26* could modulate auxin signaling through chloroplast function modification. Auxin signal can act downstream to regulate the adaptation response to light stress, as it modulates cellular pathways in cell wall flexibility and Zn homeostasis. Auxin also controls the ET/JA-mediated transcription regulation, which in turn governed by AP2/ERF transcription factors.

in photosynthesis by remodeling its apparatus against photooxidative inhibition.[13] Hence, transcriptome evidence suggests that *AtWDR26* might regulate physiological response to oxidative stress, which occurs through modulation of auxin signaling in plant cells.

Overexpression of *AtWDR26* upregulated expression of AP2/ERF transcription factors and genes involved in disease resistance (Figs. 1E and F). Among these AP2/ERF transcription factors, the expression of *C-repeat binding factor 1* (*CBF1*) and *REDOX RESPONSIVE TRANSCRIPTION FACTOR1* (*RRTF1*) was induced at 13.8 and 8.3 folds, respectively, in transgenic seedlings, which overexpress *AtWDR26*.[2] *CBF1* plays a role in the H_2O_2-triggered chloroplast retrograde signaling in response to stress.[14] The *RRTF1* transcript has a rapidly-induced switch from low light to high light conditions.[15] Ethylene (ET) and JA are 2 crucial hormones in plant cells that adapt to biotic and abiotic stress through regulation of AP2/ERF family transcription factors.[16] Transgenic seedlings overexpressing *AtWDR26* exhibited altered sensitivity to ET and JA, and upregulated gene expression involved in ET and JA synthesis.[2] The stimulating role of auxin on ethylene synthesis has been systematically studied (Abel et al., 1995). A positive relationship between the auxin and JA signal was also demonstrated, in which auxin-responsive factors like ARF6 and ARF8, and a member of the AUX/IAA family like IAA8 regulate maturation of floral organs by controlling JA synthesis.[17,18] It is plausible that increased auxin, signaling by the overexpression of *AtWDR26*, can lead to an increased defense response by the ET/JA-mediated signaling pathway. We propose that *AtWDR26* is a regulator in controlling plant growth in its response to light quality and quantity. Auxin signaling acts downstream to *AtWDR26*, and controls cellular pathways for oxidative stress protection and tolerance acquisition for biotic and abiotic stress (Fig. 2).

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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