



Response of the water–water cycle to the change in photorespiration in tobacco



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ABSTRACT

Photosynthetic electron transport produces ATP and NADPH, which are used by the primary metabolism. The production and consumption of ATP and NADPH must be balanced to maintain steady-state rates of CO₂ assimilation and photorespiration. It has been indicated that the water–water cycle (WWC) is indispensable for driving photosynthesis via increasing ATP/NADPH production. However, the relationship between the WWC and photorespiration is little known. We tested the hypothesis that the WWC responds to change in photorespiration by balancing ATP/NADPH ratio. Measurements of gas exchange and chlorophyll fluorescence were conducted in tobacco plants supplied with high (HN-plants) or low nitrogen concentration (LN-plants). The WWC was activated under high light but not low light in both HN-plants and LN-plants. HN-plants had significantly higher capacities of the WWC and photorespiration than LN-plants. Under high light, the relative high WWC activation in HN-plants was accompanied with relative low levels of NPQ compared LN-plants, suggesting that the main role of the WWC under high light was to favor ATP synthesis but not to activate NPQ. Interestingly, the activation of WWC was positively correlated to the electron flow devoted to RuBP oxygenation, indicating that the WWC plays an important role in energy balancing when photorespiration is high. We conclude that the WWC is an important flexible mechanism to optimize the stoichiometry of the ATP/NADPH ratio responding to change in photorespiration. Furthermore, HN-plants enhance the WWC activity to maintain higher rates of CO₂ assimilation and photorespiration.

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1. Introduction

Light energy is harvested by photosynthetic antenna complexes and then be used for the synthesis of ATP and NADPH, which are consumed by dark reactions including the Calvin cycle and photorespiration. Under high light, a higher rate of CO₂ assimilation results in a decrease in chloroplast CO₂ concentration, which subsequently accelerates photorespiration. The Calvin cycle and photorespiration require different ratios of ATP/NADPH [1]. Plants must finely regulate the ATP/NADPH ratio under high light, because pool sizes of ATP and NADPH are relatively small and fluxes through primary metabolism are large [2,3,4,5]. Otherwise, photosynthetic CO₂ assimilation will be depressed. For example, if ATP were consumed faster than NADPH, the lack of NADPH⁺ would rapidly induce the limitation of linear electron flow

(LEF), decreasing proton translocation and ATP synthesis. Alternatively, if NADPH were to be consumed at a greater rate than ATP, proton translocation through ATP synthase would be reduced due to limiting ADP, this would cause an increase in the proton gradient across the thylakoid membranes (ΔpH), thus, down-regulating LEF [6,7,8].

In LEF, electrons are transported from water to NADP⁺, which leads to the production of NADPH. This electron transport is coupled to proton translocation and generates a ΔpH , which drives the ATP synthesis. The stoichiometry of ATP/NADPH produced by LEF is thought to be 1.29 [9,10]. However, under current atmospheric CO₂ condition, the ATP/NADPH ratio required by primary metabolism is ~1.6 due to photorespiration [5,11]. For the key enzyme of carbon fixation Rubisco, the ratio of the carboxylation rate to the oxygenation rate is dependent on the chloroplast CO₂ and O₂ concentrations [12]. When the ratio of CO₂ to O₂ decreases in the chloroplasts, acceleration of photorespiration requires a higher ATP/NADPH demand [5]. In tobacco (*Nicotiana tabacum*), plants grown at high nitrogen concentration (HN-plants) had higher Rubisco contents and lower chloroplast CO₂ concentrations than plants grown at low nitrogen concentration (LN-plants) [13], leading to higher rates of photorespiration in HN-plants when exposed to high light. Therefore, HN-plants should have flexible mechanisms to balance the

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ATP/NADPH ratio. Cyclic electron flow around photosystem I (CEF) and water–water cycle (WWC) have been regarded as the two main mechanisms for balancing the ATP/NADPH energy budget [3,5,14,15,16,17]. Previous studies have indicated that the HN-plants enhanced CEF activity to regulate ATP/NADPH ratio and photosynthetic electron flow under high light [18,19]. However, the response of WWC activity to N supply is unclear.

The WWC channels electrons obtained from splitting of water molecules at PSII. These electrons are transported to oxygen through PSI, resulting in the formation of superoxide radicals [20,21,22]. The superoxide radicals are converted to O₂ and H₂O₂ by a membrane-attached copper/zinc superoxide dismutase (Cu/Zn SOD). Subsequently, a membrane-bound ascorbate peroxidase (thylakoid-APX) converts the hydrogen peroxide back into water [20,21,22]. The WWC under ambient conditions was regarded as a major electron sink in photosynthesis [14,15]. It has been indicated that the WWC is essential for chloroplast photoprotection in the absence and present of abiotic stresses [20,21,23,24]. Driever and Baker (2011) [25] reported that the water–water cycle in leaves was not a major alternative electron sink for dissipation of excess excitation energy when CO₂ assimilation is restricted. However, an important physiological function of the WWC is the supply of ATP for CO₂ assimilation [14,26]. In the absence of WWC, photosynthesis in algae and intact chloroplasts does not start [27]. Suppression of the WWC prolongs the induction period for CO₂ assimilation in rice leaves [14]. Therefore, the WWC activity is indispensable for driving photosynthetic CO₂ assimilation and photosynthetic electron flow in C₃ plants [26,28]. In the WWC, the formation of extra ΔpH across thylakoid membranes is not coupled with the generation of NADPH. As a result, activation of the WWC can regulate ATP/NADPH ratio. Accordingly, we speculate that HN-plants up-regulate the WWC activity to balance the ATP/NADPH ratio required by high rates of primary metabolism. By comparison, the relatively low ATP demand in LN-plants may be coupled with a low WWC activity.

Photorespiration is recognized today as an integral element of primary carbon metabolism that interacts with many other pathways [1,29]. It has been indicated that photorespiration is essential for the survival of all organisms that use Rubisco for CO₂ fixation [1,30,31,32]. Impairment of this pathway results in depression of photosynthesis and acceleration of PSII photoinhibition [33]. Photorespiratory pathway is an energy-consumption process that requires a higher ATP/NADPH ratio than the Calvin cycle [1]. Although CO₂ assimilation in the presence of photorespiration requires the extra ATP synthesis driven by the WWC [14,26], the relationship between photorespiration and the WWC activity is unclear.

The purpose of this study is to examine the response of the WWC to change in photorespiration and to clarify the role of the WWC in regulation of photosynthesis in tobacco plants grown at high or low nitrogen concentrations (HN- or LN-plants). We used gas exchange and chlorophyll fluorescence measurements to estimate the rates of electron transfer devoted to the WWC and photorespiration in HN-plants and LN-plants. The relationship between the WWC and photorespiration was examined in both type plants. Our results indicated that the WWC mainly contributed to extra ATP synthesis under high light and responded to change in photorespiration. Furthermore, HN-plants enhanced the WWC activity to balance energy demand from elevated rate of photorespiration.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Following seed germination, seedlings of tobacco cv. y87 were cultivated in a phytotron for seven weeks. Afterwards, they were grown in plastic pots in an open field at Kunming Institute of Botany, Yunnan province, China (elevation 1900 m, 102°41' E, 25°01' N). Plants were fertilized with 1000-fold diluted Hyponex 20-20-20 (Hyponex

Japan, Osaka, Japan) either three times a week or once in three weeks. During our experiment period (10 May to 27 June 2013), none of the plants experienced water stress. The average temperature at Kunming was 20.9 °C in May and 20.6 °C in June. Fully expanded mature leaves were used for photosynthetic measurements.

2.2. Gas Exchange and Chlorophyll Fluorescence Measurements

Photosynthetic parameters for gas exchange and chlorophyll fluorescence were monitored synchronously with an open gas exchange system that incorporated infrared CO₂ and water vapor analyzers (Li-6400XT; Li-Cor Biosciences, Lincoln, NE, USA) and a 2-cm² measuring head (6400–40 Leaf Chamber Fluorometer; Li-Cor Biosciences). Measurements were made in a phytotron where relative air humidity (60%) and air temperature (25 °C) were controlled. The atmospheric CO₂ concentration was maintained at 400 μmolmol⁻¹ by the Li-6400XT. To generate a light response curve, we initially exposed the mature leaves to strong irradiance (2000 μmol photons m⁻² s⁻¹) for 20 min to obtain steady-state high levels of g_s and CO₂ assimilation rate. Afterward, photosynthetic parameters were evaluated at 2-min intervals at photosynthetic photon flux densities (PPFDs) of 2000, 1500, 1200, 800, 500, 300, 200, 100, 50, 20, or 0 μmol photons m⁻² s⁻¹.

The fluorescence parameters F_m , F_m' , and F_s were evaluated as previously described in Baker and Rosenqvist (2004) [34]. Here, F_m and F_m' represented the maximum fluorescence after dark-adaptation and light-adaptation, respectively. F_m was measured after one night dark adaptation. F_s indicated the light-adapted steady-state fluorescence. The effective quantum yield of PSII (Φ_{PSII}) was calculated as $\Phi_{PSII} = (F_m' - F_s)/F_m'$ [35]. Non-photochemical quenching (NPQ) was computed as $NPQ = (F_m - F_m') / F_m'$.

2.3. Estimation of Photosynthetic Electron Flow

The NADPH demands from CO₂ assimilation and photorespiration were calculated according to the models of Farquhar et al. (1980) [12]. From the data from gas exchange measurements, the rate of electron transport for NADPH required by carboxylation and oxygenation of RuBP (J_g) was calculated as follows [5,36]:

$$J_g = 4 \times (A_n + R_d) \times (C_i + 2^*) / (C_i - \Gamma^*)$$

where A_n represents the measured CO₂ assimilation rate, R_d represents the rate of mitochondrial respiration measured after 30 min dark adaptation, C_i is the intercellular CO₂ concentration, and Γ^* is the CO₂ compensation point in the absence of day respiration, assumed to be 32.2 at 25 °C [37].

The electron transport using the data obtained by chlorophyll fluorescence measurements (J_{PSII}) was computed as:

$$J_{PSII} = PPFD \times \Phi_{PSII} \times dII \times p$$

where PPFD represents the incident photosynthetic photons flux density, Φ_{PSII} represents the effective quantum yield of PSII, dII represents the distribution ratio of light absorbed by chloroplast to PSII and is assumed to be 0.51 and 0.42 in HN-plants and LN-plants, respectively [18], and p represents the ratio of light absorbed by chloroplasts and is assumed to be 0.85 and 0.72 in HN-plants and LN-plants, respectively [18].

The electron flow devoted to RuBP oxygenation (J_o) or RuBP carboxylation (J_c) was calculated according to the method of Valentini et al. (1995) [38]:

$$J_c = 1/3 \times (J_{PSII} + 8 \times (A_n + R_d))$$

$$J_o = 2/3 \times (J_{PSII} - 4 \times (A_n + R_d)).$$

The alternative electron flow devoted to the WWC was calculated as follows [36]:

$$J_a = J_{PSII} - J_g.$$

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