



The relationship between photosystem II efficiency and quantum yield for CO₂ assimilation is not affected by nitrogen content in apple leaves

Lailiang Cheng^{1,3}, Leslie H. Fuchigami² and Patrick J. Breen²

¹ Department of Horticulture, 134A Plant Science Building, Cornell University, Ithaca, NY 14853-4203, USA

² Department of Horticulture, Oregon State University, Corvallis, OR 97331, USA

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Abstract

Bench-grafted Fuji/M.26 apple (*Malus domestica* Borkh.) trees were fertigated with different concentrations of nitrogen by using a modified Hoagland's solution for 45 d. CO₂ assimilation and photosystem II (PSII) quantum efficiency in response to incident photon flux density (PFD) were measured simultaneously in recent fully expanded leaves under low O₂ (2%) and saturated CO₂ (1300 µmol mol⁻¹) conditions. A single curvilinear relationship was found between true quantum yield for CO₂ assimilation and PSII quantum efficiency for leaves with a wide range of leaf N content. The relationship was linear up to a quantum yield of approximately 0.05 mol CO₂ mol⁻¹ quanta. It then became curvilinear with a further rise in quantum yield in response to decreasing PFD. This relationship was subsequently used as a calibration curve to assess the rate of non-cyclic electron transport associated with Rubisco and the partitioning of electron flow between CO₂ assimilation and photorespiration in different N leaves in response to intercellular CO₂ concentration (C_i) under normal O₂ conditions. Both the rate of non-cyclic electron flow and the rate of electron flow to CO₂ or O₂ increased with increasing leaf N at any given C_i. The percentage of non-cyclic electron flow to CO₂ assimilation, however, remained the same regardless of leaf N content. As C_i increased, the percentage of non-cyclic electron flow to CO₂ assimilation increased. In conclusion, the relationship between PSII quantum efficiency and quantum yield for CO₂ assimilation and the partitioning of electron flow between CO₂ assimilation and photorespiration are not affected by N content in apple leaves.

Key words: Apple, *Malus domestica*, CO₂ assimilation, electron partitioning, leaf N content, non-photochemical quenching, PSII efficiency, quantum yield.

Introduction

Light-driven photosynthetic electron transport provides reducing power for photosynthetic carbon reduction and photorespiratory carbon oxidation. Both these processes are associated with the activity of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco). Electron transport may also provide a source for alternative electron sinks, such as nitrate reduction and direct reduction of O₂ in the Mehler reaction. Genty *et al.* first found a linear relationship between quantum yield for CO₂ assimilation and the product of photochemical quenching (qP) and the efficiency of excitation capture (F_v'/F_m') by open photosystem II (PSII) centres under non-photorespiratory conditions (Genty *et al.*, 1989). This provides the basis for using $qP \times F_v'/F_m'$ (PSII quantum efficiency) to monitor changes in quantum yield of non-cyclic electron transport *in vivo*. The quantitative relationship between PSII quantum efficiency and quantum yield for CO₂ assimilation, developed under non-photorespiratory conditions, has subsequently been used as a calibration curve to estimate the rate of non-cyclic electron transport associated with Rubisco and partitioning of electron flow between CO₂ assimilation and photorespiration under photorespiratory conditions (Cornic and Briantais, 1991; Cornic and Ghashghaie, 1991; Ghashghaie and Cornic, 1994; Habash *et al.*, 1995).

The relationship between PSII quantum efficiency and quantum yield for CO₂ assimilation or O₂ evolution

³To whom correspondence should be addressed. Fax: +1 607 255 0599. E-mail: LC89@Cornell.edu

has been well documented. Linear relationships have been reported in many species (Cornic and Briantais, 1991; Cornic and Ghashghaie, 1991; Genty *et al.*, 1989, 1992; Ghashghaie and Cornic, 1994; Harbinson *et al.*, 1990; Keiller and Walker, 1990; Krall and Edwards, 1990, 1991; Krall *et al.*, 1991; Maxwell *et al.*, 1998). However, the relationship became non-linear in the high quantum yield region or at low measuring PFD (Öquist and Chow, 1992; Seaton and Walker, 1990). It appears that the relationship between PSII quantum efficiency and quantum yield for CO₂ assimilation is conserved as it holds across species (Seaton and Walker, 1990) and is not affected by water stress or elevated CO₂ (Cornic and Ghashghaie, 1991; Habash *et al.*, 1995).

The effect of leaf N on the relationship between PSII quantum efficiency and quantum yield for CO₂ assimilation has not been closely examined. Khamis *et al.* noted a small decrease in quantum yield for CO₂ assimilation at any given PSII efficiency in maize (*Zea mays* L.) leaves under low N supply (Khamis *et al.*, 1990). The decrease in light absorption caused by N limitation, however, may not have been taken into account. Both *in vivo* Rubisco activity and PSII quantum efficiency are closely co-ordinated in apple (*Malus domestica* Borkh.) leaves in response to nitrogen supply. Although total Rubisco activity increased with increasing leaf N, Rubisco activation state decreased so that only a proportion of the total Rubisco was engaged in photosynthesis in high N leaves (Cheng and Fuchigami, 2000). Under high PFD conditions, the PSII quantum efficiency of apple leaves was down-regulated by increased thermal dissipation in response to decreasing leaf N, to match Rubisco activity (Cheng *et al.*, 2000). However, it remains unclear how leaf N affects the rate of electron flow associated with Rubisco and its partitioning between CO₂ assimilation and photorespiration in apple leaves.

The objectives of this study were to (1) determine the relationship between PSII quantum efficiency and quantum yield for CO₂ assimilation in response to leaf N under non-photorespiratory conditions; and (2) assess the partitioning of non-cyclic electron flow between CO₂ assimilation and photorespiration in relation to N in apple leaves.

Materials and methods

Plant material

'Fuji' apple (*Malus domestica* Borkh.) trees on M.26 rootstocks were used. Bench-grafting was done in late March, and each grafted tree was immediately put into a 3.8 l pot containing a mixture of peat moss, pumice and sandy loam soil (1 : 2 : 1, by vol.). The plants were grown in a lathhouse until early June. During this period, beginning from budbreak in early May, they were fertigated every 2 weeks with 10.7 mM N using Plantex[®] 20 N-10 P₂O₅-20 K₂O with micronutrients (Plantex Corp., Ontario, Canada). When new shoots were approximately

15 cm long, plants were selected for uniformity, and moved out to full sunlight. Thereafter, they were fertigated weekly with Plantex[®] for 3 weeks. Beginning 30 June, plants were fertigated twice weekly with one of six levels of N concentrations (0, 2.5, 5, 7.5, 10, or 15 mM N from NH₄NO₃) by applying 300 ml of a modified Hoagland's solution to each pot (Cheng and Fuchigami, 2000). Irrigation was provided from a saucer placed at the bottom of each pot. After 45 d, recent fully expanded leaves at the same developmental stage across the treatments were selected for gas exchange and chlorophyll fluorescence measurements.

Measurements of gas exchange and chlorophyll fluorescence

CO₂ assimilation and chlorophyll fluorescence were measured simultaneously using a system that combined a CIRAS-1 gas exchange system (PP Systems, Herts., UK) and an FMS-1 pulse-modulated fluorometer (Hansatech Instruments Ltd., Norfolk, UK). The light- and temperature-controlled cuvette of the CIRAS-1 system was modified as follows: the fibre optic of the FMS-1 was inserted into the cuvette at a 60° angle without significantly interfering with PFD distribution at the leaf surface, yet it allowed for delivery of a saturation pulse of actinic light and detection of fluorescence signals. All gas exchange measurements were made at a leaf temperature of 25 ± 0.2 °C.

The relationship between quantum yield for CO₂ assimilation and PSII quantum efficiency was studied by altering incident PFD. Measurements of CO₂ assimilation and chlorophyll fluorescence parameters in response to PFD were made in descending order, at incident PFDs of 1990, 1614, 1242, 891, 593, 398, 255, 160, or 87 μmol m⁻² s⁻¹ at the leaf surface level, as measured with a recently calibrated LI-190SA quantum sensor (Li-Cor Inc., Lincoln, Nebraska, USA). At each PFD, CO₂ assimilation, stomatal conductance, and steady-state fluorescence (F_s) were monitored to ensure that they reached a steady-state before a reading was taken. Maximal fluorescence under light exposure (F'_m) was obtained by imposing a 1 s saturating flash to the leaf in order to reduce all the PSII centres. Minimal fluorescence (F'_0) under light exposure was determined by covering the cuvette with a black cloth while a far-red light was switched on to oxidize PSII rapidly by drawing electrons from PSII to PSI. Maximal fluorescence (F_m) and minimal fluorescence (F_0) of dark-adapted leaves were measured pre-dawn.

Non-photochemical quenching (NPQ) was expressed as $F_m/F'_m - 1$ (Stern-Volmer quenching; see Bilger and Björkman, 1990). The efficiency of excitation capture by open PSII centres (F'_v/F'_m) was calculated as $(F'_m - F'_0)/F'_m$, which is also referred to as the efficiency with which excitation energy is transferred to open PSII centres. The photochemical quenching coefficient qP was defined as $(F'_m - F_s)/(F'_m - F'_0)$. PSII quantum efficiency was $(F'_v/F'_m)qP = (F'_m - F_s)/F'_m$ (Genty *et al.*, 1989). Quantum yield for CO₂ assimilation was calculated as gross CO₂ assimilation ($A + R_d$) divided by either incident PFD or absorbed PFD. R_d was day respiration under light from processes other than photorespiration, which was approximated as dark respiration for this experiment. Leaf absorptance was measured with a LI-1800 Spectroradiometer and an 1800-12S Integrating Sphere (Cheng *et al.*, 2000).

Partitioning of non-cyclic electron flow between CO₂ assimilation and photorespiration in leaves with different N contents was studied by measuring responses of CO₂ assimilation and PSII quantum efficiency to intercellular CO₂ concentrations (C_i) at normal O₂ (21%) conditions. Response curves of CO₂ assimilation and PSII quantum efficiency to C_i were constructed at an incident PFD of 1000 μmol m⁻² s⁻¹ by

altering air CO_2 concentrations (C_a) from 50 to 1200 ~ 1400 $\mu\text{mol mol}^{-1}$ in 9 or 10 steps, until the highest C_i reached approximately 1000 $\mu\text{mol mol}^{-1}$. At each C_a , readings of CO_2 assimilation, stomatal conductance, and steady-state fluorescence were taken after they all reached steady state. PSII quantum efficiency was measured as described above.

The rate of non-cyclic electron transport associated with Rubisco and its partitioning to CO_2 assimilation and photorespiration were calculated (Ghashghaie and Cornic, 1994). Briefly, the quantitative relationship between quantum yield for CO_2 assimilation and PSII quantum efficiency, developed under non-photorespiratory conditions, was used as a calibration curve. Quantum yield for CO_2 assimilation (Φ_{CO_2}) obtained from the calibration curve corresponding to the PSII quantum efficiency measured under photorespiratory conditions allows the rate of non-cyclic electron flow (J_L) to be calculated as $J_L = \Phi_{\text{CO}_2} \times \text{PFD} \times 4$. The rate of electron flow to CO_2 assimilation (J_A) and to photorespiration (J_o) were calculated as $J_A = 4(A + R_d)$, and $J_o = J_L - J_A$, respectively.

Leaf N content

After all the above measurements, leaf area was determined with a LI-3000 Area Meter. Leaves were frozen at -80°C , then freeze-dried. N content was determined via the Kjeldahl method (Schuman *et al.*, 1973).

Results

The relationship between quantum yield for CO_2 assimilation and PSII quantum efficiency under non-photorespiratory conditions

As PFD increased, CO_2 assimilation increased almost linearly first, then reached a saturation point (Fig. 1A), beyond which CO_2 assimilation showed little response to increasing PFD. Both true quantum yield for CO_2 assimilation (Fig. 1B) and PSII quantum efficiency (Fig. 1C) decreased with increasing PFD. At each given PFD, CO_2 assimilation, true quantum yield for CO_2 assimilation, and PSII quantum efficiency all decreased as leaf N decreased.

Chlorophyll fluorescence quenching parameters in response to incident PFD are shown in Fig. 2. As PFD increased, non-photochemical quenching (NPQ) increased, then tended to level off with further increases in PFD (Fig. 2A). Correspondingly, the efficiency of excitation capture by open PSII centres (F_v'/F_m') decreased with increasing PFD (Fig. 2B). The photochemical quenching coefficient (qP) also decreased with increasing PFD (Fig. 2C). At each given PFD, NPQ increased with decreasing leaf N (Fig. 2A), resulting in a corresponding decline in F_v'/F_m' (Fig. 2B); qP also decreased with decreasing leaf N content (Fig. 2C). The decline in both F_v'/F_m' and qP in response to increasing PFD led to the fall in PSII quantum efficiency (Fig. 1C). At each given PFD, the decrease in both F_v'/F_m' and qP also contributed to a decline in PSII quantum efficiency with decreasing leaf N content (Fig. 1C).

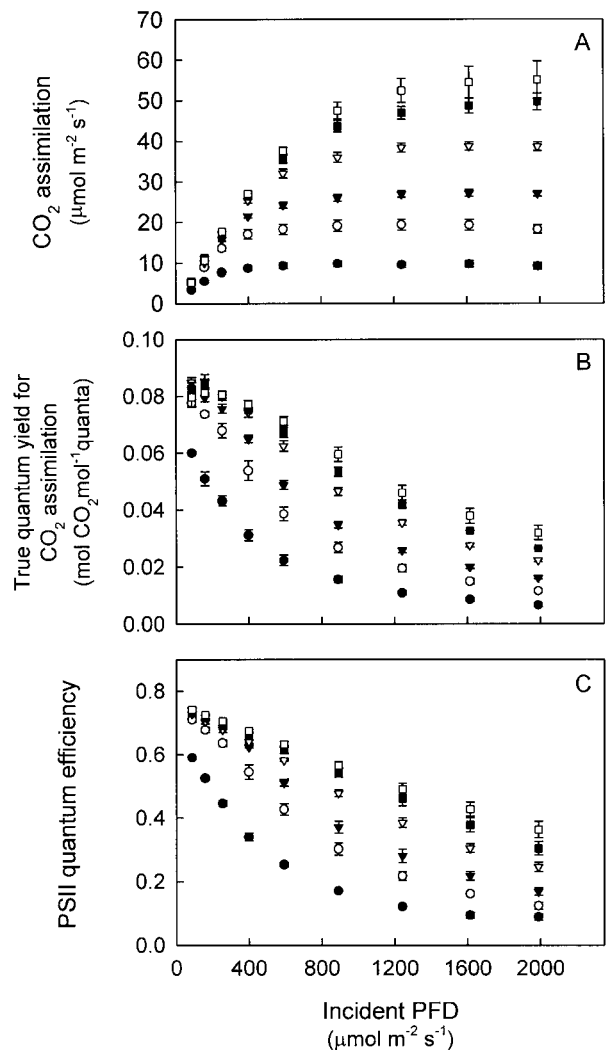


Fig. 1. CO_2 assimilation (A), true quantum yield for CO_2 assimilation (B), and PSII quantum efficiency (C) of apple leaves in response to incident photon flux density (PFD) under low O_2 (2%) and saturated CO_2 (1300 $\mu\text{mol mol}^{-1}$) conditions. Measurements were made at leaf temperature of $25 \pm 0.2^\circ\text{C}$ and ambient water vapour pressure of 1.37 ± 0.15 kPa. Each data point represents the average of three replications with standard error. Leaf N content (g m^{-2}) is: 1.022 ± 0.077 (●); 1.566 ± 0.065 (○); 1.802 ± 0.10 (▼); 2.361 ± 0.031 (▽); 3.227 ± 0.011 (■); and 4.044 ± 0.207 (□).

When each fluorescence parameter (NPQ , F_v'/F_m' , and qP) was plotted against the true quantum yield for CO_2 assimilation (Fig. 3), curvilinear relationships to true quantum yield for CO_2 assimilation were found for NPQ , F_v'/F_m' , and qP (Fig. 3A, B, C, respectively). In response to rising PFD or decreasing leaf N, NPQ increased. This resulted in a decrease in F_v'/F_m' . A decline in qP also contributed to the lowering of quantum yield for CO_2 assimilation in response to rising PFD or decreasing leaf N.

A close relationship was found between quantum yield for CO_2 assimilation and PSII quantum efficiency (Fig. 4). At any given PSII efficiency, low N leaves had

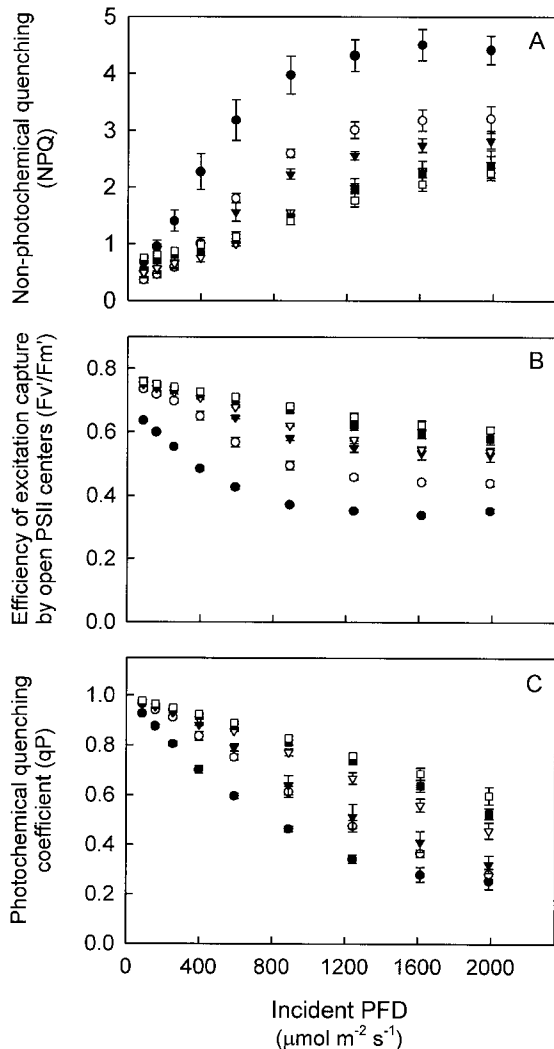


Fig. 2. Non-photochemical quenching (A), efficiency of excitation capture by open PSII centres (B), and photochemical quenching (C) of apple leaves in response to incident photon flux density (PFD) under low O₂ (2%) and saturated CO₂ (1300 μmol mol⁻¹) conditions. Measurement conditions and symbols are the same as in Fig. 1.

a slightly lower apparent quantum yield for CO₂ assimilation (Fig. 4A). However, when quantum yield was expressed on an absorbed PFD basis (i.e. true quantum yield), all the data points from leaves with different N contents nearly fell into a single line (Fig. 4B). The relationship was linear up to a true quantum yield of approximately 0.05 mol CO₂ mol⁻¹ quanta. It then became curvilinear with a further rise in quantum yield in response to decreasing PFD.

Partitioning of electron flow to CO₂ assimilation and photorespiration in response to intercellular CO₂ concentration (C_i)

As C_i increased, CO₂ assimilation increased linearly first, then reached a plateau (Fig. 5A). Both the initial slope

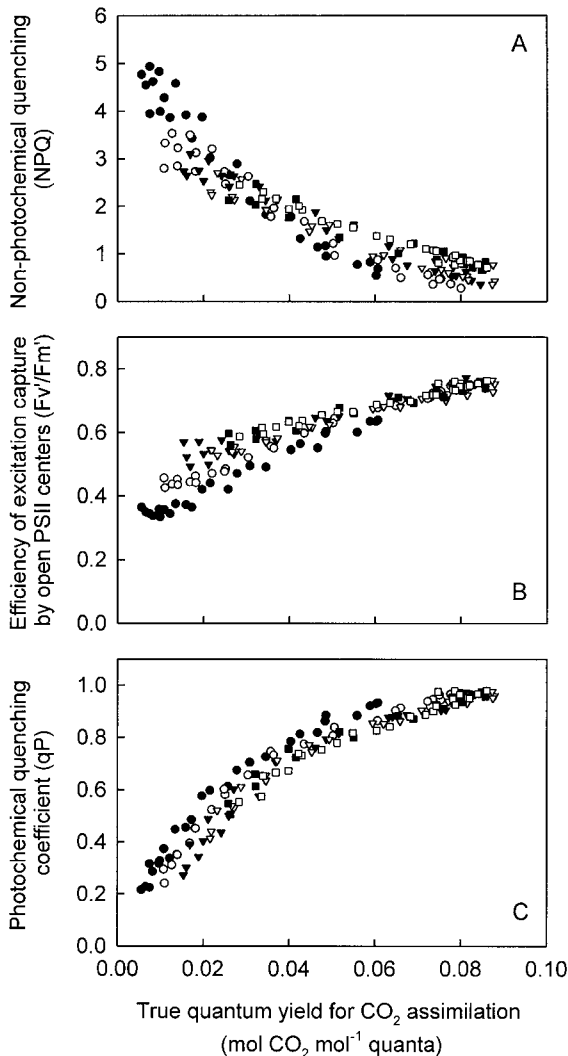


Fig. 3. True quantum yield for CO₂ assimilation in relation to chlorophyll fluorescence quenching parameters in apple leaves under low O₂ (2%) and saturated CO₂ (1300 μmol mol⁻¹) conditions. (A) Non-photochemical quenching (NPQ); (B) efficiency of excitation capture by open PSII centres (F_v'/F_m'); and (C) photochemical quenching coefficient (qP). Symbols are the same as in Fig. 1 except that each data point represents a single measurement.

and the maximum CO₂ assimilation increased with increasing leaf N. PSII quantum efficiency showed a response to C_i similar to that of CO₂ assimilation, but reached a plateau at a lower C_i (Fig. 5B). This was most obvious for high N leaves. Using the curve in Fig. 4B, it was possible to estimate the rate of non-cyclic electron transport associated with Rubisco under photorespiratory conditions. Non-cyclic electron transport followed almost the same pattern as PSII quantum efficiency in response to C_i. At any given C_i, non-cyclic electron transport increased with increasing leaf N (Fig. 5C).

Non-cyclic electron flow to CO₂ showed the same response to C_i as had CO₂ assimilation (Fig. 6A). As C_i increased, electron flow to CO₂ increased almost linearly

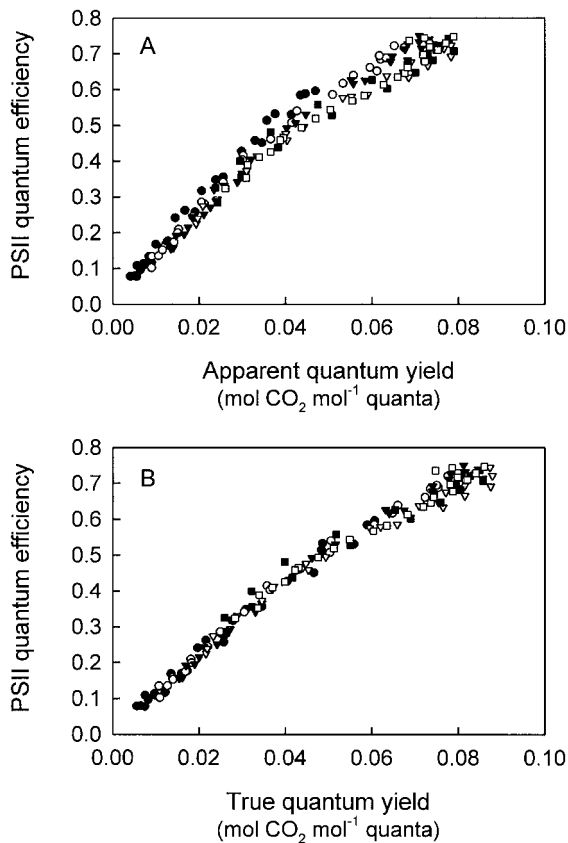


Fig. 4. PSII quantum efficiency in relation to apparent quantum yield (A) and true quantum yield (B) for CO₂ assimilation in apple leaves under low O₂ (2%) and saturated CO₂ (1300 μmol mol⁻¹) conditions. Symbols are the same as in Fig. 1 except that each data point represents a single measurement.

first, then levelled off with a further rise in C_i . At any given C_i , electron flow to CO₂ was higher in high-N than in low-N leaves, although the difference was smaller at lower than at higher C_i (Fig. 6A). Non-cyclic electron flow to O₂ generally decreased as C_i increased (Fig. 6B). The difference in electron flow to O₂ at different N contents was larger at lower than at higher C_i . As C_i dropped below about 100 μmol mol⁻¹, a decrease in non-cyclic electron flow to O₂ was noticed in medium to high-N leaves, but not in low-N leaves (Fig. 6B). When the electron flow to CO₂ was expressed as a percentage of non-cyclic electron flow, all data for leaves with different N contents nearly fell on one curve (Fig. 6C). As C_i increased, an increasing proportion of the non-cyclic electron flow was partitioned to CO₂ assimilation.

Discussion

Photosynthetic electron transport drives both Rubisco-associated CO₂ assimilation and photorespiration, and also supplies electrons to other alternative electron sinks. A single curvilinear relationship was found between true quantum yield for CO₂ assimilation and PSII quantum

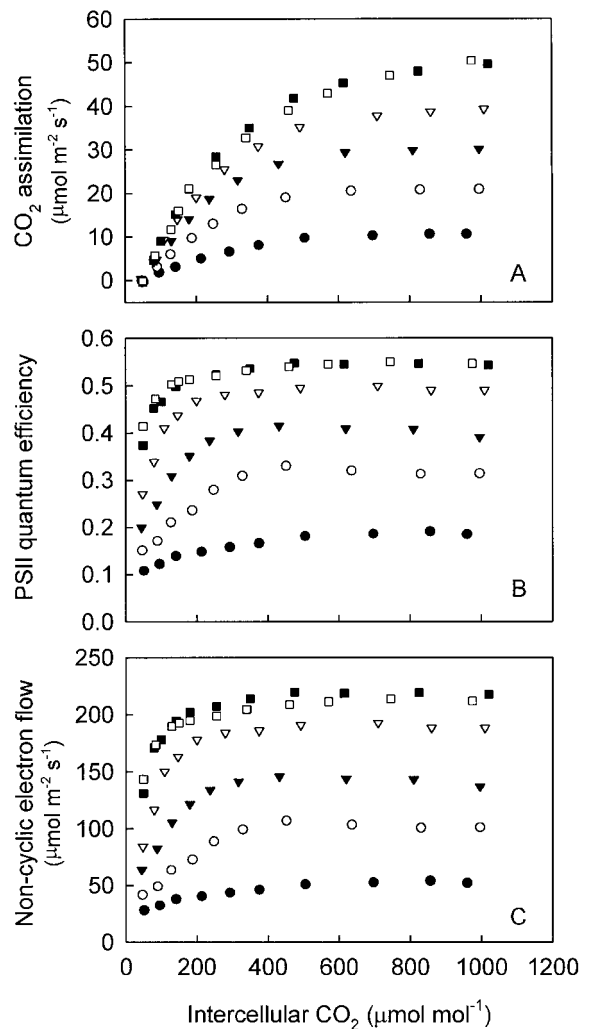


Fig. 5. CO₂ assimilation (A), PSII quantum efficiency (B), and total non-cyclic electron transport (C) of apple leaves in response to intercellular CO₂ concentration at 21% O₂. Measurements were made at incident PFD of 1000 μmol m⁻² s⁻¹, leaf temperature of 25 ± 0.2 °C, and ambient water vapour pressure of 1.45 ± 0.1 kPa. Leaf N content (g m⁻²) is: 1.10 (●); 1.53 (○); 1.99 (▼); 2.32 (▽); 3.22 (■); and 3.81 (□).

efficiency in apple leaves with different N contents under non-photorespiratory conditions (Fig. 4B). Based on this relationship, partitioning of non-cyclic electron flow between CO₂ assimilation and photorespiration was examined in response to C_i , as affected by leaf N. At any given C_i , the percentage of total non-cyclic electron flow to CO₂ assimilation remained unchanged regardless of leaf N content (Fig. 6C). Therefore, the relationship between PSII quantum efficiency and quantum yield for CO₂ assimilation under non-photorespiratory conditions, and the partitioning of non-cyclic electron flow between CO₂ assimilation and photorespiration at normal O₂ conditions, are not affected by N content in apple leaves.

The slope of the relationship between quantum yield for CO₂ assimilation and PSII quantum efficiency depends on the partitioning of non-cyclic electron flow

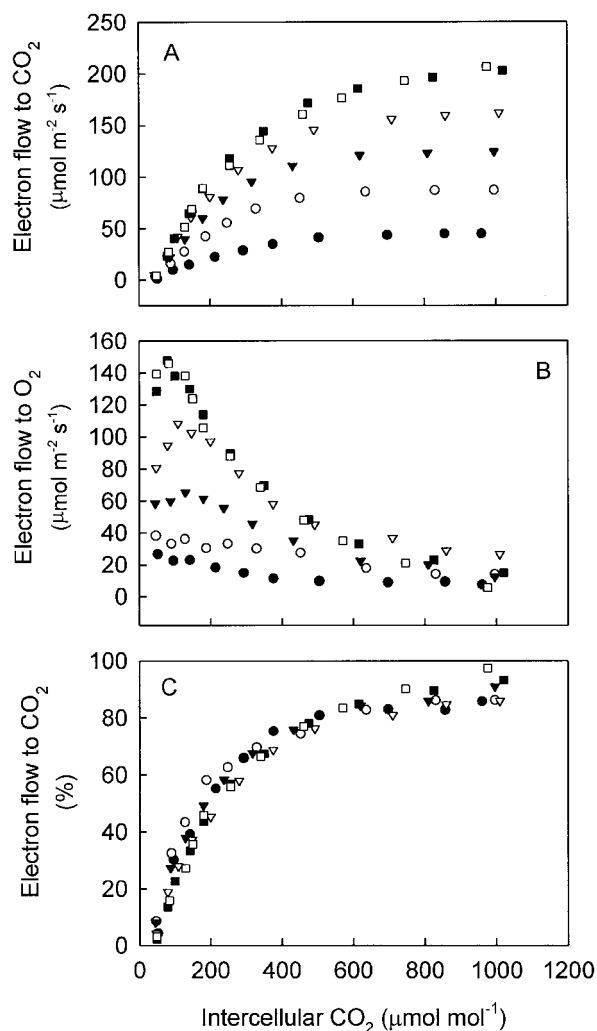


Fig. 6. Partitioning of total non-cyclic electron flow to CO₂ assimilation and photorespiration of apple leaves in response to intercellular CO₂ concentration at 21% O₂: electron flow to CO₂ (A); electron flow to O₂ (B); and percentage of electron flow to CO₂ (C). Measurement conditions and symbols are the same as in Fig. 5.

between CO₂ assimilation and other alternative electron sinks under non-photorespiratory conditions. At any given PSII efficiency, if other electron sinks use more reducing power, the quantum yield for CO₂ assimilation would be reduced.

Among the alternative electron sinks, nitrate reduction can consume up to 8% of the total non-cyclic electron flow (Evans, 1987). In addition to serving as a substrate in photorespiration, O₂ also functions as an electron acceptor in the Mehler reaction (Badger, 1985). Although nitrate reduction primarily occurs in the root system of apple trees, nitrate reductase activity has been detected in leaves as the nitrate supply increases (Lee and Titus, 1992). This altered proportion of nitrate reduction in apple leaves in response to N supply, or a possible increase of the Mehler reaction in low N leaves under high light, could change the slope of the relationship.

However, in this study, a single curvilinear relationship was found between PSII quantum efficiency and true quantum yield for CO₂ assimilation in apple leaves with different N contents. This indicates that leaf N content does not affect the partitioning of non-cyclic electron flow to CO₂ assimilation relative to alternative electron sinks under non-photorespiratory conditions. The observed decrease in apparent quantum yield for CO₂ assimilation at any given PSII efficiency was mainly caused by failing to account for the decrease in light absorption in low N leaves.

The curvilinear relationship found between quantum yield for CO₂ assimilation and PSII quantum efficiency in this study is similar to that noted earlier (Seaton and Walker, 1990; Öquist and Chow, 1992). The exact cause for this non-linearity is unclear, but several factors may contribute. These include PSII heterogeneity (Hormann *et al.*, 1994; Schreiber *et al.*, 1995), changes in electron cycling around PSII and partitioning of non-cyclic electron flow to processes other than CO₂ assimilation (Genty *et al.*, 1989), and approximation of day respiration with dark respiration (Oberhuber *et al.*, 1993). In addition, non-linearity could occur if chlorophyll fluorescence and gas exchange measurements were monitoring different populations of leaf cells.

In this study the effects of non-photochemical and photochemical quenching on quantum yield for CO₂ assimilation were clearly seen. Increased NPQ in response to increasing incident PFD or decreasing leaf N caused a decline in quantum yield for CO₂ assimilation by decreasing the efficiency with which excitation energy was transferred to open PSII centres (Figs 2A, B, 3A, B). At high PFD, especially in low-N leaves when NPQ reached its maximum activity (Fig. 2A), F_v/F_m decreased to its minimum and no longer responded to increasing PFD (Fig. 2B). As qP decreased in response to increasing PFD or decreasing leaf N (Fig. 2C), PSII quantum efficiency was reduced (Fig. 1C). Therefore, it is both non-photochemical and photochemical quenching that determine PSII quantum efficiency (Genty *et al.*, 1989).

The quantitative relationship between PSII efficiency and CO₂ assimilation obtained under non-photorespiratory conditions served as a calibration curve in this study. This curve was used to estimate the rate of non-cyclic electron transport associated with Rubisco and its partitioning between CO₂ assimilation and photorespiration under photorespiratory conditions. It was assumed that alternative electron sinks accounted for the same proportion of total non-cyclic electron transport under both photorespiratory and non-photorespiratory conditions. Both the rate of non-cyclic electron flow associated with Rubisco and the rate of electron flow to CO₂ and to O₂ increased with increasing leaf N at any given C_i. However, the percentage of non-cyclic electron flow to CO₂ assimilation remained the same regardless

of leaf N content. This indicates that electron partitioning between CO₂ assimilation and photorespiration is not affected by leaf N content. For a given C_i, apple leaves with different N contents may be operating at a similar CO₂ concentration at the carboxylation site of Rubisco. This is because the ratio of carboxylation to oxygenation is mainly determined by the actual concentrations of CO₂ and O₂ within the chloroplasts at a given temperature and atmospheric pressure (Brooks and Farquhar, 1985; Jordan and Ogren, 1984).

The partitioning of non-cyclic electron flow between CO₂ assimilation and photorespiration in response to C_i in apple leaves found in this study is consistent with the result obtained by measuring ¹⁸O₂ uptake and net ¹⁶O₂ evolution in leaves of C₃ plants (Badger, 1985; Canvin *et al.*, 1980; Gerbaud and Andre, 1980). In those studies, a decrease in O₂ uptake at low CO₂ concentrations was reported. It is interesting that in this study electron flow to O₂ decreased when C_i dropped below about 100 μmol mol⁻¹ in medium to high-N leaves, but not in low N-leaves. This decrease could be caused by deactivation of Rubisco at low CO₂ concentrations (Badger, 1985). Indeed, Rubisco activation state falls substantially when C_i drops below 100 μmol mol⁻¹ (Sage *et al.*, 1990; von Caemmerer and Edmondson, 1986). The differential response of non-cyclic electron flow to O₂ at low C_i in apple leaves with different N contents in this study could have been caused by the difference in the amount of active Rubisco. In low-N leaves, the amount of Rubisco is very limited, and all the Rubisco is active at ambient CO₂ (Cheng and Fuchigami, 2000). When C_i decreases to below 100 μmol mol⁻¹, the amount of CO₂ may be adequate to keep all the Rubisco activated in low-N leaves. In contrast, the same low C_i may activate only a percentage of the Rubisco in medium to high-N leaves.

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