

Relationship between allocation of absorbed light energy in PSII and photosynthetic rates of C₃ and C₄ plants

Jen-Hsien Weng

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Abstract Two C₃ dicotyledonous crops and five C₄ monocotyledons treated with three levels of nitrogen were used to evaluate quantitatively the relationship between the allocation of absorbed light energy in PSII and photosynthetic rates (P_N) in a warm condition (25–26°C) at four to five levels [200, 400, 800, 1,200 (both C₃ and C₄) and 2,000 (C₄ only) $\mu\text{mol m}^{-2} \text{s}^{-1}$] of photosynthetic photon flux density (PPFD). For plants of the same type (C₃ or C₄), there was a linear positive correlation between the fraction of absorbed light energy that was utilized in PSII photochemistry (P) and P_N , regardless of the broad range of their photosynthetic rates due to species-specific effect and/or nitrogen application; meanwhile, the fraction of absorbed light energy that was dissipated through non-photochemical quenching (D) showed a negative linear regression with P_N for each level of PPFD. The intercept of regression lines between P and P_N of C₃ and C₄ plants decreased, and that between D and P_N increased with increasing PPFD. With P and D as the main components of energy dissipation and complementary to each other, the fraction of excess absorbed light energy (E) was unchanged by P_N under the same level of PPFD. At the same level of P_N , C₄ plants had lower P and higher D than C₃ plants, due to the fact that C₄ plants with little or no photorespiration is considered a limited energy sink for electrons. Nevertheless there was a

significant negative linear correlation between D and P when data from both C₃ and C₄ plants at varied PPFD levels was merged. The slope of regression lines between P and D was 0.85, indicating that in plants of both types, most of the unnecessary absorbed energy (ca. 85%) could dissipate through non-photochemical quenching, when P was inhibited by low P_N due to species-specific effect and nitrogen limitation at all levels of illumination used in the experiment.

Keywords C₃ · C₄ · Chlorophyll fluorescence · Energy dissipation · Photosynthetic rate

Abbreviations

D	The fraction of absorbed light energy dissipated through non-photochemical quenching
E	The fraction of excess absorbed light energy
N	Nitrogen
P	The fraction of absorbed light energy utilized in PSII photochemistry
P_N	Photosynthetic rate
PPFD	Photosynthetic photon flux density
PSII	Photosystem II

Introduction

Sunlight is the energy source for plant photosynthesis. However, in habitats fully exposed to sun, leaves in the top canopy layer may absorb more photons than they can utilize, and this excessively absorbed energy often leads to a reduced efficiency of PSII (Demmig-Adams et al. 1996; Kato et al. 2003; Hikosaka et al. 2004). Plants utilize several mechanisms, including heat dissipation via xanthophylls cycle, to alleviate the damage caused by

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J.-H. Weng (✉)
 Graduate Institute of Ecology and Evolutionary Biology,
 China Medical University, Taichung, Taiwan
 e-mail: jhweng@mail.cmu.edu.tw

J.-H. Weng
 Department of Life Science, National Chung-Hsing University,
 Taichung, Taiwan

absorbing excess light energy (Li et al. 2000; Morosinotto et al. 2001; Holt et al. 2005). Therefore, the light absorbed in PSII antennae can be divided to (1) that utilized in photosynthesis, (2) that dissipated by photo-protective mechanisms and (3) the excess light energy that is neither utilized nor dissipated (Demmig-Adams et al. 1996). While the utilization of absorbed energy is closely related to the photosynthetic efficiency, this efficiency may also be depressed by the excess light energy (Demmig-Adams et al. 1996; Kato et al. 2003; Hikosaka et al. 2004). Therefore, an estimate of the allocation of absorbed light energy is important for a comprehensive understanding of the photosynthetic efficiency of plants (Demmig-Adams et al. 1996; Kato et al. 2002, 2003).

Chlorophyll fluorescence measurement, a fast and non-invasive technique, has been widely used to monitor the functional changes of photosynthesis apparatus under different conditions (Demmig-Adams et al. 1996; Verhoeven et al. 1997, 1998). Demmig-Adams et al. (1996) proposed a simple model of chlorophyll fluorescence parameters to approximate energy partitioning to photochemistry and heat dissipation. The fraction of absorbed light energy that is utilized in PSII photochemistry (P) can be estimated from chlorophyll fluorescence parameter, $P = \Delta F/F_m'$; the fraction of absorbed light energy that is dissipated thermally (D) can be estimated from $D = 1 - F_v'/F_m'$; and the fraction of excess absorbed light (E) can be estimated from $E = 1 - P - D$. Since photosynthetic CO_2 assimilation is the major sink for absorbed light energy, the difference in both light intensity and leaf photosynthetic rate may lead to different allocation of photons absorbed by the photosystem (Demmig-Adams et al. 1996; Kato et al. 2003; Hikosaka et al. 2004). Under the same level of light intensity, plant leaves with lower photosynthetic capacities, due to genotype or stress conditions, showed lower P but higher D than leaves with higher photosynthetic capacities (Demmig-Adams et al. 1996; Kato et al. 2003). With high light intensity, plants could dissipate the excess light energy efficiently via xanthophylls cycle, in which violaxanthin is de-epoxidized into antheraxanthin and zeaxanthin. Therefore, even photosynthetic rate increased with an increased intensity of light shone on the leaf, P usually decreases, and D as well as E increases (Demmig-Adams et al. 1996; Oliveria and Peñuelas 2001; Kato et al. 2003). From what is mentioned above, it is understood that, the relationship between the allocation of absorbed light energy and photosynthetic rate may be varied with light intensity. But it has not yet been quantitatively evaluated.

In addition, photorespiration is considered as another mechanism to affect the dissipation of excess energy (Osmond 1981; Kozaki and Takeba 1996; Park et al. 1996).

Unlike C_3 plants, C_4 plants display little or no photorespiration, and therefore, are supposed to have lower energy consumption for photosynthesis (Krall et al. 1991; Peterson 1994; Carmo-Silva et al. 2008). It has also been pointed out that the ratio of quantum yields of PSII to CO_2 fixation in C_3 plants is higher than that in C_4 plants under normal atmospheric conditions (Oberhuber and Edwards 1993; Peterson 1994; Ripley et al. 2007). This decrease in efficiency in utilizing energy derived from PSII for CO_2 fixation is due to photorespiration. The above results indicate that the relationship between photosynthetic rate and P could vary between C_3 and C_4 plants; nevertheless, there have been few studies on the allocation of absorbed light energy into D and E of C_4 plants (Demmig-Adams et al. 1996; Oliveria and Peñuelas 2001; Kato et al. 2003; Hikosaka et al. 2004). Besides, nitrogen (N) is an important nutrient factor for photosynthesis. Chloroplasts contain 70–80% of the cell N (Makino and Osmond 1991), it includes enzymes and photosynthetic performance requires proteins for all steps of the process, including formation of the light-harvesting chlorophyll–protein complexes of the antenna (Makino and Osmond 1991; Bungard et al. 1997). Therefore, photosynthetic capacity is known to be generally proportional to leaf N content (Bolton and Brown. 1980; Sage and Pearcy 1987; Makino and Osmond 1991; Cheng et al. 2000; Kato et al. 2002, 2003). Due to their CO_2 concentrating mechanism, the photosynthetic rate per unit leaf N of C_4 plants is usually higher than that of C_3 plants (Bolton and Brown 1980; Sage and Pearcy 1987; Ripley et al. 2008).

Because the relationship between photosynthetic rate and the allocation of absorbed light energy under varied light intensity has not been quantitatively evaluated, let alone a comparison of plants with a broad range of photosynthetic capacity, including C_3 and C_4 plants under varied light intensity and N. In the current study, pertinent parameters of two C_3 and five C_4 plants with treatments of different levels of N and under varied light intensity, i.e. plants with a broad range of photosynthetic capacity, were measured to assess the relationship between the photosynthetic rate and the allocation of absorbed energy.

Materials and methods

Plant materials

Two C_3 dicotyledonous crops [Chinese kale (*Brassica oleracea* L.) and sweet potato (*Ipomoea batatas* (L.) Lam.)] and five C_4 herbaceous monocotyledons [maize (*Zea mays* L. NADP-ME sub-type), napier grass (*Pennisetum purpureum* Schum., NAD-ME), Guinea grass (*Panicum maximum* Jacq., PEP-CK), *Setaria viridis* (L.)

P. Beauv. (NADP-ME) and *Miscanthus floridulus* (Labill) Warb. ex Schum: & Laut, (NADP-ME)] were used in this study. All these species were potted (38 cm-diameter) in a mixture of soil:vermiculite:sand = 1:1:1, and placed outdoors to receive regular water and full sunlight on the campus of National Chung-Hsing University (24°10'N, 78 m), Taichung, Taiwan. Each species was given three levels of N (0, 5 and 15 mM week⁻¹) for 2 weeks.

Measurements of photosynthetic rate and chlorophyll fluorescence

From April to May 2004 (air temperature ca. 25–26 °C), attached and fully expanded upper leaves were used for the measurements of photosynthetic rate (P_N) and chlorophyll fluorescence. P_N was measured with a portable, open-flow gas exchange system (LI-6400, LI-COR, Lincoln, NE, USA) connected to a leaf chamber (6400-02B, LI-COR) and LED light source (6400-02, LI-COR). Measurements were made at 200, 400, 800, 1,200 (both C₃ and C₄) and 2,000 (C₄ only) $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD), ambient temperature/humidity and CO₂ concentration.

After photosynthesis measurement, the same light levels were used to measure chlorophyll fluorescence. First, the plants were acclimated in a dark room (room temperature ca. 25°C) for at least 20 min; and the dark-acclimated chlorophyll fluorescence was measured with a portable pulse amplitude modulated fluorometer (PAM-2000, Walz, Effeltrich, Germany). Then, the adaxial surfaces of measured leaves were illuminated stepwise from low to high levels of PPFD by a slide projector with halogen light source, i.e., 200, 400, 800, 1,200 (both C₃ and C₄) and 2,000 (C₄ only) $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 20 min; and light-acclimated fluorescence measurement was made with the same equipment as in the dark. Each leaf was measured four to five times and means of these measurements were used in statistical analyses. PPFD was measured by a LI-190SA quantum sensor (LI-COR, USA).

Calculation of photosystem II efficiency and energy dissipation

The fraction of absorbed light energy that is dissipated thermally was calculated as $D = 1 - F_v'/F_m' = 1 - (F_m' - F_0')/F_m'$. While the light energy utilized in PSII photochemistry was estimated as $P = \Delta F/F_m' = (F_m' - F)/F_m'$, the excess was calculated from $E = 1 - P - D$ (Demmig-Adams et al. 1996; Kato et al. 2003). F_m and F_m' are the maximal fluorescence, and F_0 and F_0' are the minimal fluorescence in dark-adapted (20 min or more) and illuminated (measured after far-red illumination) leaves, respectively. F is the actual level of fluorescence during illumination.

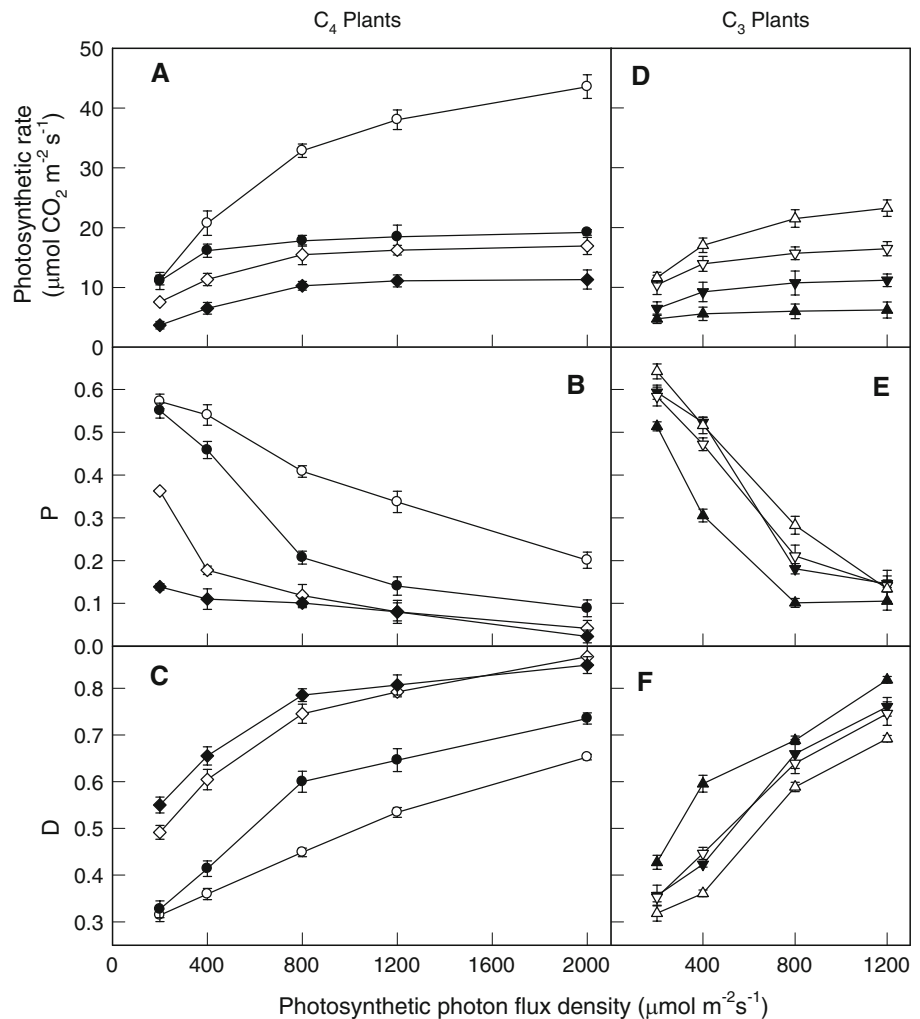
Results and discussion

Figure 1 shows the typical light-response curve of P_N , P and D for C₃ and C₄ plants under varying PPFD, with the maximum P_N ranging between 6 and 24 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for C₃ plants at 1,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Figs. 1d, 2d), and between 9 and 44 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for C₄ plants at 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Figs. 1a, 2e). In general, high N-treated C₄ leaves showed highest P_N , which was not saturated even at 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Fig. 1a). On the contrary, N-limited C₃ leaves showed the lowest P_N and light saturation point (Fig. 1d). However, *Miscanthus*, a wild C₄ grass, showed both low P_N and light saturation point even under high N treatment (Fig. 1a; Weng and Hsu 2001). Figure 1 also shows that P decreased but D increased, in general, with increasing illumination; and leaves with higher P_N always showed higher P but lower D than leaves with lower P_N .

We merged the results of all measured leaves in the same type of plants (C₃ or C₄), and the allocations of absorbed light energy for these plants are shown in Figs. 2, 3, 4. In both C₃ and C₄ plants, P and P_N always had a linear positive correlation while D showed a negative linear regression with P_N for each level of PPFD. Compared at the same level of P_N and PPFD, P of C₃ plants was higher than that of C₄ plants while D of C₃ plants was lower than that of C₄ plants (Figs. 2, 3). The intercept of regression lines between P and P_N of C₃ and C₄ plants decreased (Figs. 2, 5a), and that between D and P_N increased (Figs. 3, 5b) with increasing PPFD. In addition, the intercepts between P and P_N of C₃ plants were higher, and those between D and P_N were lower than those of C₄ plants under low to medium PPFD (Fig. 5a, b). Slopes of these regression lines showed the same tendency as intercepts, except for C₃ plants under low PPFD (200 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Figs. 2, 3, 5c, d). Most E of both C₃ and C₄ plants ranged from 0.05 to 0.25, and there was no significant correlation with P_N , but with a slight increase with PPFD (Fig. 4). Yet, slopes of the regression lines between E and P_N were near 0 under each level of PPFD.

Generally plant leaves with lower photosynthetic capacities, due to genotype or stress conditions, showed lower P but higher D than leaves with higher photosynthetic capacities under the same level of light intensity (Demmig-Adams et al. 1996; Kato et al. 2003). With high light intensity, plants could dissipate the excess light energy efficiently via xanthophylls cycle, in which violaxanthin is de-epoxidized into antheraxanthin and zeaxanthin. Therefore, even photosynthetic rate increased with the intensity of light shone on the leaf increases, P decreases and D as well as E increases usually (Demmig-Adams et al. 1996; Oliveria and Peñuelas 2001; Kato et al. 2003). The results of the present study (Figs. 1, 2, 3) indicate that, in

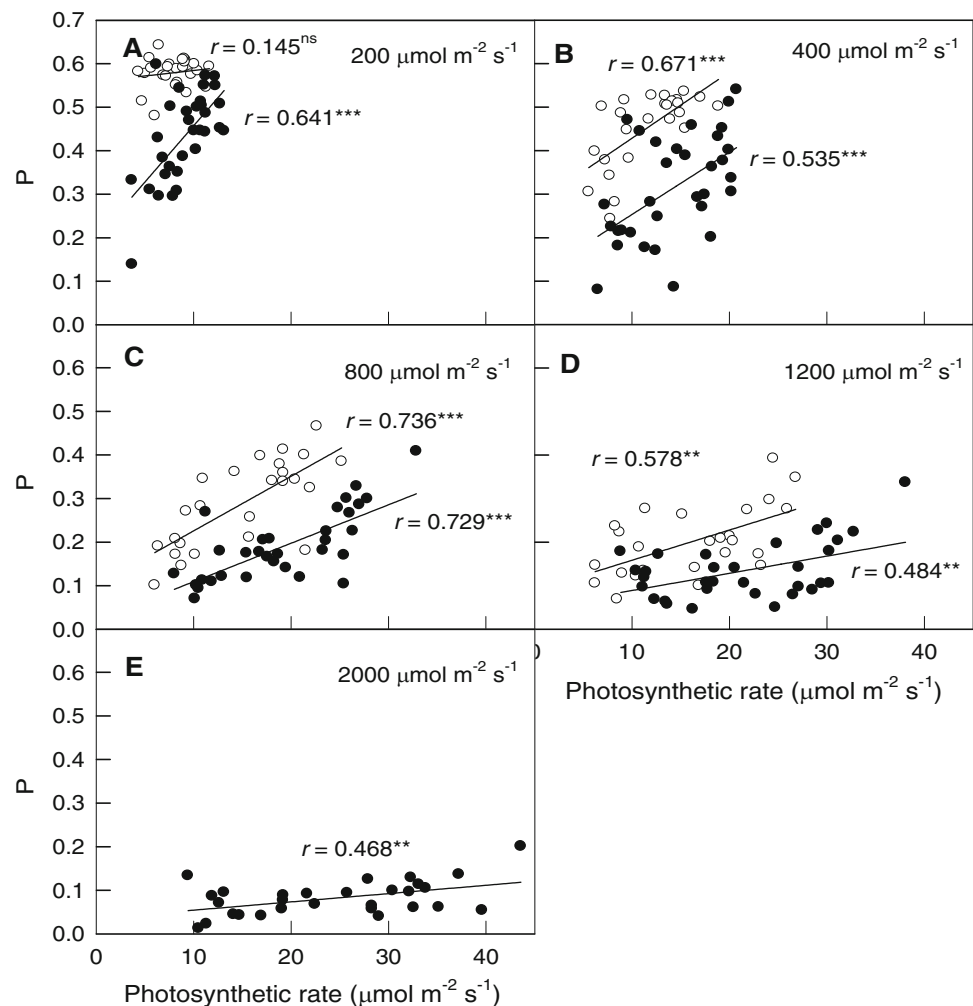
Fig. 1 Typical light-response curve of photosynthetic rate, fraction of light energy absorbed in photosystem II that is utilized in photochemistry (P) and dissipated thermally (D) of C_3 and C_4 plants under varied photosynthetic photon flux density. Different symbols indicate different leaves, triangle symbols represent C_3 plants, cycle symbols represent maize (C_4 plant), diamond symbols represent *Miscanthus* (C_4 plant), open symbols represent nitrogen treatment, and close symbols represent nitrogen limited. Vertical bars indicate the standard errors



both C_3 and C_4 plants, P always decreased, and D always increased with increasing illumination. It also shows that, under the same level of illumination, leaves with a lower photosynthetic capacity always exhibited lower quantum yield of PSII and higher portion of non-photochemical quenching. These results have been reported previously (Demmig-Adams et al. 1996; Gamon et al. 1997; Oliveria and Peñuelas 2001; Kato et al. 2003; Guo and Trotter 2004). However, Figs. 2, 3 show that the allocation of absorbed light energy to P and D was correlated with P_N , when all data in the same type of plants (C_3 or C_4) were compiled for statistical analysis, in spite of the broad range of photosynthetic capacity in these species and different levels of N application; and the intercept and slope of the regression lines between P and P_N as well as between D and P_N of C_3 and C_4 plants were related to the PPFD level (Figs. 2, 3, 5). Thus, the relationship between photosynthetic rate and the allocation of absorbed light energy under varied light intensity could be quantitatively evaluated. These findings have not been reported previously in detail.

Leaf N is a major factor that determines the photosynthetic capacity of plants. Both chlorophyll content and total Rubisco activity (Evans and Terashima 1987; Cheng et al. 2000) as well as photosynthetic capacity (Bolton and Brown 1980; Sage and Pearcy 1987; Makino and Osmond 1991; Cheng et al. 2000; Kato et al. 2002, 2003) decrease with decreasing leaf N, and Rubisco decreases more than thylakoid proteins (Evans and Terashima 1987). Since the major sink for absorbed light energy of plants is photosynthetic carbon assimilation, a lower photosynthetic capacity may lead to a higher portion of excess energy. However, it was reported that both xanthophyll cycle pool size and the conversion of violaxanthin to zeaxanthin under high irradiance are enhanced in response to N limitation in order to dissipate excessive absorbed light (Verhoeven et al. 1997; Cheng 2003). As a result, P and photosynthetic capacity decrease, and D or non-photochemical quenching increases under N limitation (Verhoeven et al. 1997; Cheng et al. 2000; Cheng 2003; Kato et al. 2003), leading to a similar (Kato et al. 2003) or slight increase of E

Fig. 2 Relationships between photosynthetic rate and allocation of light energy absorbed in photosystem II that is utilized in photochemistry (P) of C_3 (open circle, two species) and C_4 (filled circle, five species) plants at each level (200–2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) of photosynthetic photon flux density. Each species was applied with three levels of nitrogen. Each point in a panel is the measured value of each leaf. *ns*, ** and *** represent not significant, $P < 0.01$ and $P < 0.001$, respectively



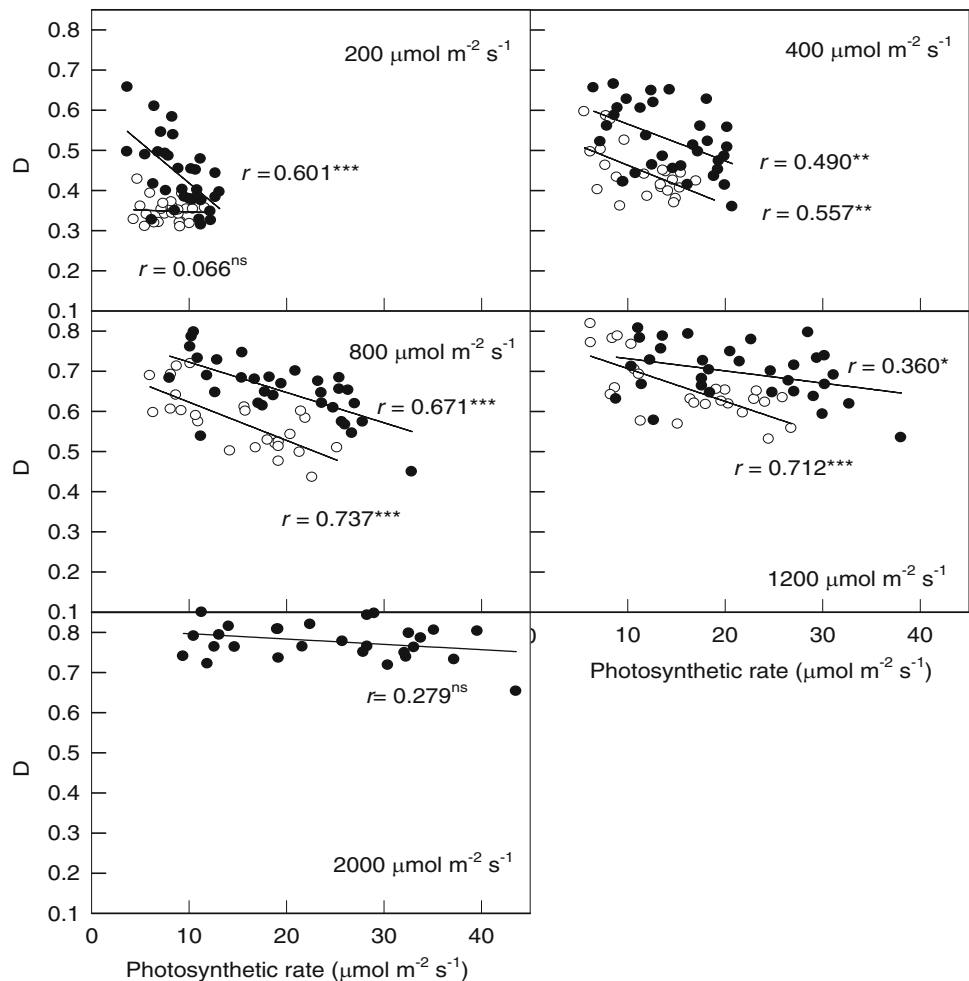
(Verhoeven et al. 1997). The same tendency reported by Kato et al. (2003) is also observed in the present study, namely, P and P_N always had a linear positive correlation (Fig. 2) while D showed a negative (Fig. 2) linear regression with P_N for each level of PPFD. Since P and D are the main components of energy dissipation and complementary to each other when P_N changed (Figs. 2, 3), E was not affected by P_N under the same level of PPFD (Fig. 4).

Photorespiration is another sink for absorbed light energy (Osmond 1981; Kozaki and Takeba 1996; Park et al. 1996), and C_4 plants, with little or no photorespiration, is considered as a limited energy sink for electrons (Krall et al. 1991; Peterson 1994; Ripley et al. 2007). Thus, generally, C_4 plants exhibited a higher photosynthetic rate and a lower ratio of quantum yield of PSII to CO_2 fixation than C_3 plants under normal atmospheric conditions (Oberhuber and Edwards 1993; Peterson 1994; Ripley et al. 2007). Therefore, Figs. 2 and 3 show that C_4 plants had lower P , but higher D than C_3 plants when leaves with the same level of P_N were compared under the same level of PPFD. Decreasing O_2 partial pressure from ambient levels

(approximately 20 kPa) to approximately 2 kPa could increase up to ca. twofold the net rate of CO_2 fixation in C_3 plants as a result of reduced photorespiration (Oberhuber and Edwards 1993; Peterson 1994). At the same time the quantum yield of PSII of C_3 plants decreased by ca. 50% (Peterson 1994). Results of the present study have shown that the maximum P_N of C_4 plants was ca. 1.1 (at 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD) to 1.5 (at 1,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD) folds higher than that of C_3 plants, and P of C_4 plants was ca. 1.2–1.6-fold lower than that of C_3 plants (Fig. 2). This is similar to the observations of Peterson (1994), i.e., C_4 plants showed a higher photosynthetic rate and a lower P than C_3 plants because the former, having little or no photorespiration, represent limited energy sink (Krall et al. 1991; Peterson 1994).

Even though C_4 plants always show a higher P_N and a lower P than C_3 plants, due to nil or lower energy consumption from photorespiration (Figs. 1, 2), the present study indicates that D showed a significant negative linear correlation with P when data from C_3 and C_4 plants at varied levels of PPFD were merged and analyzed (Fig. 6).

Fig. 3 Relationships between photosynthetic rate and allocation of light energy absorbed in photosystem II that is dissipated thermally (D) of C_3 (open circle, two species) and C_4 (filled circle, five species) plants at each level (200–2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) of photosynthetic photon flux density. Each species was applied with three levels of nitrogen. Each point in a panel is the measured value of each leaf. *ns*, *, ** and *** represent not significant, $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively



This result suggests that, even C_3 and C_4 plants were merged for statistical analysis, P and D are still complementary to each other; and C_3 and C_4 plants could dissipate similar portions of the unnecessary absorbed energy through non-photochemical quenching. Because C_4 plants have little energy consumption for photosynthesis, they generally display a lower P and higher D than C_3 plants under the same P_N level (Figs. 2, 3). Regression analysis in Fig. 6 also shows that slopes of regression lines between P and D was 0.85, indicating when the fraction of absorbed light utilized in PSII photochemistry was inhibited, most (about 85%) of the unnecessary absorbed energy could dissipate through non-photochemical quenching (P), leading to a similar level of excess absorbed light energy (E) in both C_3 and C_4 plants under all tested conditions. Besides, similar to previously reports (Oliveria and Peñuelas 2001; Kato et al. 2003; Hikosaka et al. 2004), Fig. 4 shows that E was increased slightly with PPFD, due to more excessive absorbed light. However, the variation of E under different levels of PPFD was not high; and D still showed a significant negative

linear correlation with P when data from all tested leaves at varied levels of PPFD were merged (Fig. 6). In addition, during winter, there was a decrease of P and an increase of D and E (Hovenden and Warren 1998; Oliveria and Peñuelas 2001; Sveshnikov et al. 2006); and the correlation between D and P varied with species as well as cold-hardening (Hovenden and Warren 1998). In this study, the experiment was made in a warmer condition (25–26°C); presumably, the relationship between D and P shown in Fig. 6 may vary at lower temperatures.

Other factors, such as mesophyll diffusion rate of CO_2 or stomatal conductance, can also affect photosynthetic capacity (Gale 1972; Terashima et al. 1993; Weng and Hsu 2001). These two factors and leaf N content may account for the species difference of photosynthetic capacity. It was also reported that species with a lower photosynthetic capacity always showed lower quantum yield of PSII (Gamon et al. 1997; Guo and Trotter 2004), and higher portion of non-photochemical quenching (Guo and Trotter 2004). The same tendency has been observed herein since the plants used in this work had a broad range of

Fig. 4 Relationships between photosynthetic rate and allocation of light energy absorbed in photosystem II that is excess absorbed light energy (E) of C_3 (open circle, two species) and C_4 (filled circle, five species) plants at each level (200–2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) of photosynthetic photon flux density. Each species was applied with three levels of nitrogen. Each point in a panel is the measured value of each leaf. *ns* represents not significant

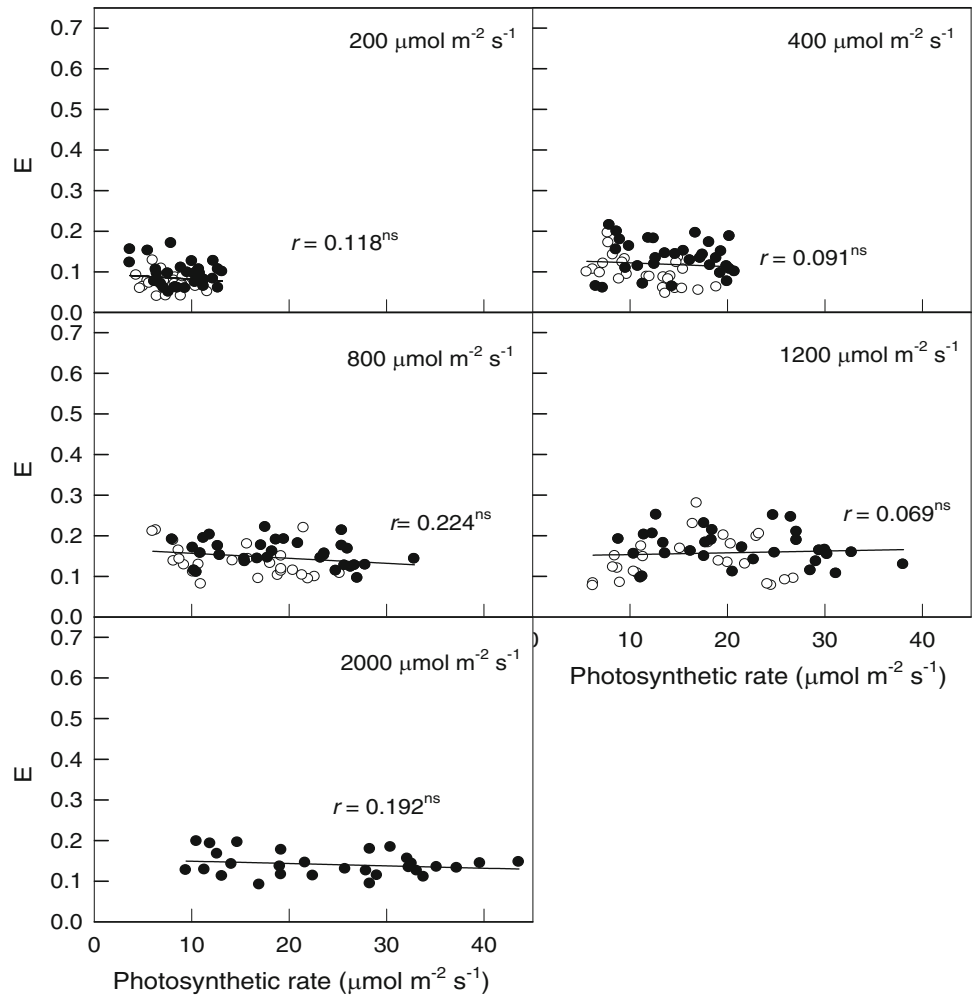
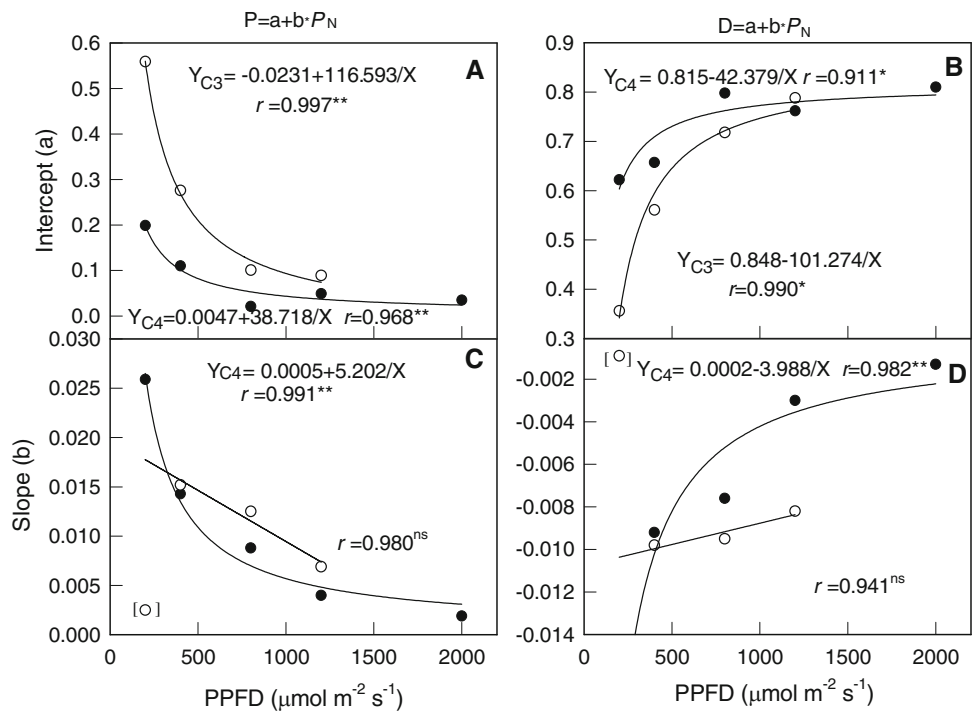


Fig. 5 The intercept and slope of the regression lines between photosynthetic rate (P_N), and allocation of light energy absorbed in photosystem II that is utilized in photochemistry (P , from Fig. 2), dissipated thermally (D , from Fig. 3) of C_3 (open circle) and C_4 (filled circle) plants changing with photosynthetic photon flux density (PPFD). *ns*, * and ** represent non-significant, $P < 0.05$ and $P < 0.01$, respectively; open circle represents data excluding measurement at 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD



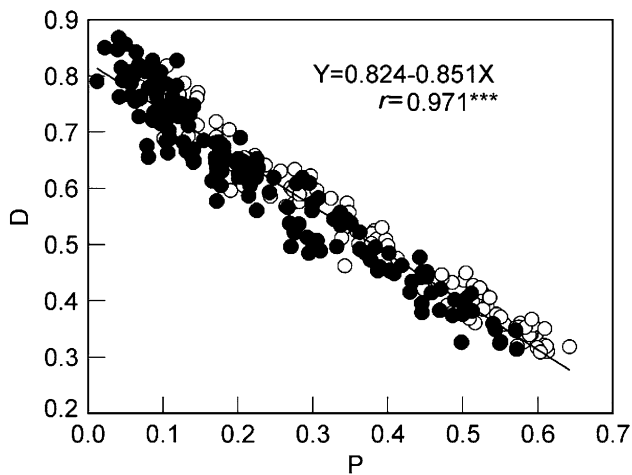


Fig. 6 Relationship between allocation of light energy absorbed in photosystem II that is utilized in photochemistry (P) and dissipated thermally (D) of C_3 (open circle, two species) and C_4 (filled circle, five species) plants. Each species was applied with three levels of nitrogen and measured at varied photosynthetic photon flux density (C_3 plants $200\text{--}1,200\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, C_4 plants $200\text{--}2,000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$). Each point is the measured values of each leaf at a certain level of photosynthetic photon flux density. *** represents $P < 0.001$

photosynthetic capacity due to species-specific effect and N application.

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