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Photosynthetic responses to CO_2 concentration and photon fluence rates in the CAM-cycling plant *Delosperma tradescantioides* (Mesembryanthemaceae)

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SUMMARY

Responses of gas exchange and photosynthesis to changes in CO_2 concentration and PPFD were examined in well watered plants of *Delosperma tradescantioides* Bgr. to establish the relative importance of these environmental changes on the photosynthetic machinery in this CAM-cycling species which grows naturally in both exposed and partly shaded environments. Plants were grown at two PPFDs (220 [LL] and 550 [HL] μmol m^{-2} s^{-1}). HL plants had larger leaves with higher specific weight, water content and diurnal malic acid fluctuation. Photosynthetic PPFD responses were typically those of sun and shade species for HL and LL plants, both under 21 % O_2 and non-photorespiratory (2 % O_2) conditions. The CO_2 compensation point in the absence of non-photorespirational CO_2 evolution in the light (Γ_*) was *c.* 30 μmol mol^{-1}. Irradiation reduced mitochondrial respiration by > 50 %. Comparison of the PPFD responses of linear electron flow rates derived from gas exchange measurements and from fluorescence analysis (J_F) indicated effective photosynthetic control. J_F was always larger than electron flow rates calculated from gas exchange, indicating that processes other than carboxylation and oxygenation were consistently important in energy consumption under all sampled environmental conditions. Regardless of PPFD during growth, electron flow to carboxylation and J_F were linearly correlated, demonstrating that the photosynthetic apparatus was well adapted to PPFD during growth. In HL plants, non-photochemical quenching increased, and photochemical quenching and the quantum yield of linear electron transport through PS II decreased more slowly with increasing PPFD than in LL plants. In plants of both treatments non-photochemical energy dissipation seemed to be exhausted when the proportion of photons not utilizable by photochemistry exceeded 0·7. Results illustrate a pronounced ability of *D. tradescantioides* to acclimate to a 100 % change in the prevailing PPFD and lend support to the hypothesis that CAM cycling might act as a photoprotective process.

Key words: Crassulacean acid metabolism, CAM-cycling, *Delosperma tradescantioides* Bgr., photorespiration, photosynthetic electron flow, photoprotection.

INTRODUCTION

In CAM plants the capacity to accumulate malic acid (Δ-malate) at night might be directly related to the efficiency of photosynthetic CO_2 assimilation of the preceding light period (Nobel, 1988). When there is sufficient photosynthesis, a large amount of carbohydrate is provided as a precursor of phosphoenolpyruvate at night, and the malic acid pool is depleted completely, thus improving the sink capacity of the vacuoles. In CAM plants exposed to a highly dynamic light environment this relationship is largely affected by PPFD during growth (Fetene, Lee & Lüttge, 1990; Lüttge *et al.*, 1991; Maxwell, Griffiths & Young, 1994). On the other hand, CAM

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has been assumed to act as a photoprotective mechanism (Adams & Osmond, 1988; Roberts *et al.*, 1996). Therefore, rather precise knowledge of the photosynthetic characteristics is necessary to understand fully the ecological significance and the potential limitations of CAM.

Delosperma tradescantioides, a prostrate, weedy perennial succulent grows exposed or semi-exposed in the eastern coastal plain and inland areas of southern Africa, which have summer and all-year rainfall (Herppich *et al.*, 1996). When well watered, *D. tradescantioides* exhibits all features of CAM-cycling (Herppich *et al.*, 1996). Plants then exclusively take up CO_2 during the day. This is, however, coupled with a low but significant Δ-malate (Herppich *et al.*, 1996) as is typical for CAM-cycling (Martin, 1996). During a drought, *D. tradescantioides* reversibly switches to CAM-idling (Herppich *et al.*, 1996), i.e. carbon uptake is inhibited both day and night but nocturnal accumulation of malic acid still occurs. As this shift can occur virtually overnight, it is unlikely that the photosynthetic machinery is altered in the short term. Therefore, *D. tradescantioides* provides a valuable tool for the detailed investigation of the photosynthetic characteristics in CAM plants, which is not easily possible in obligate CAM plants due to pronounced variations in both stomatal conductance and internal CO_2 concentration.

Using CO_2/H_2O gas exchange and fluorescence analysis techniques, we investigated the characteristics of photosynthesis to develop a more comprehensive understanding of the photosynthetic performance of *D. tradescantioides* in relation to available PPFD. This enables us to analyse the possible photoprotective function of CAM in this flexible CAM species. We were especially interested in the photosynthetic performance of plants adapted to low- and high PPFD with different investments in light harvesting machinery and carboxylation capacity. This information allows the development of a detailed model of photosynthesis, which enables us to characterize the effects of drought on photosynthesis in *D. tradescandioides* for further investigation.

MATERIALS AND METHODS

Plant material and growth conditions

Two groups of plants of *Delosperma tradescantioides* Bgr., raised from cuttings, were grown in plastic pots (0·5 l of garden soil and sand, 1:1) under controlled conditions (day: temperature (T) = 28 ± 3 °C, r.h. = 35 ± 5 %; night: T = 18 ± 2 °C, r.h. = 75 ± 5 %) in a glasshouse. They were watered on alternate days and fertilized twice a month. Natural light was supplemented (12 h) by high-pressure mercury-vapour lamps (Power Star® HQI-TS 250 W/D; Osram, München, Germany) to give a minimum PPFD of *c.* 220 (LL) or 450 μmol m^{-2} s^{-1} (HL) at plant level.

Three wk before the start of the experiment, HL plants were transferred into a growth chamber (Ecophyt Model VEPHQ 5/1350, Heraeus-Voetsch, Balingen, Germany) with a PPFD of 550 μmol m^{-2} s^{-1} (12 h). In a second study several LL plants were brought into the growth chamber where they experienced *c.* 460 μmol m^{-2} s^{-1} only shortly before measurements. Air temperature was 25 °C during the day and 15 °C at night at a dewpoint of *c.* 12 °C. All plants were watered daily during the measurement periods.

Gas-exchange measurements

The gas exchange of whole twigs (six to eight leaves) was determined with an open system (Minicuvette®, H. Walz GmbH, Effeltrich, Germany) fitted with a humidity control by-pass. CO_2 exchange was measured with an IRGA (BINOS 4b.2, Fisher-Rosemount GmbH u. Co., Hanau, Germany), and the humidity of the air stream entering and leaving the assimilation chamber determined with dewpoint mirrors (H. Walz GmbH, Effeltrich, Germany). The desired CO_2 and O_2 mole fractions of the air were obtained with a standard gas mixing unit (H. Walz GmbH, Effeltrich, Germany), and CO_2 concentration was controlled by an IRGA working in the absolute mode (BINOS 4b.1). Gas exchange parameters, calculated (von Willert, Matyssek & Herppich, 1995) from data continuously recorded by a computer at 5-min intervals, were based on total leaf surface (*c.* double the projected leaf area) as leaves are amphistomatous.

For determination of PPFD dependence of photosynthesis, leaves were illuminated from overhead by a special light source, comprising four halogen lamps (Masterline Dichr., 38°, 50 W, 12 V; Phillips, Germany). PPFD was varied using optically neutral plastic foil screens fixed to the top of the assimilation chamber.

Electron flow rates required to satisfy both carboxylation and oxygenation ($\mathcal{J}_{CO}$) and those necessary to satisfy total ATP consumption ($\mathcal{J}_{CA}$) were estimated using the formulations derived by von Caemmerer & Farquhar (eqns 8 and 9, 1981), as follows:

$$\mathcal{J}_{CO} = 4 \times \frac{C + 2\Gamma_*}{C - \Gamma_*} \times A^* \quad (1)$$

and

$$\mathcal{J}_{CA} = 4{\cdot}5 \times \frac{C + \frac{7}{3}\Gamma_*}{C - \Gamma_*} \times A^*, \quad (2)$$

where C represents the CO_2 mole fraction in the stroma and Γ_* the CO_2 compensation point in the absence of non-photorespirational CO_2 evolution in the light (= 'day respiration', R_d). A^* indicates the

CO_2 assimilation rate of the illuminated leaf side and was computed as $2(\mathcal{J}_{CO_2}+R_d)$. R_d and Γ_* were estimated as explained in 'Results', C was assumed to be 70 % of c_i (von Caemmerer & Evans, 1991). Note that electron flow rates were always related to the projected leaf area. The theoretical minimum electron flow used for carbon assimilation ($\mathcal{J}_{cm}$) was computed on a leaf area basis as $4A^*$ (Krall & Edwards, 1992).

Fluorescence analysis

Chlorophyll fluorescence was monitored simultaneously with gas exchange (PAM fluorometer, H. Walz GmbH, Effeltrich, Germany) on leaves of the same plant enclosed in a black plastic clamp and dark-adapted for 20 min. After measuring the initial (F_0) and the maximum fluorescence (F_m), the latter being obtained with a saturating light pulse (0·8 s, 5·7 mmol m^{-2} s^{-1}; KL1500 cold light source, Schott, Wiesbaden, Germany), actinic white light was provided at the desired intensity by a second KL1500 cold light source. Additional saturating pulses were applied every 60 s to yield the maximum fluorescence during illumination (F'_m). Fluorescence was monitored for 15 min until the terminal steady state fluorescence (F_t) was attained. Relaxation of dark fluorescence was followed for *c*. 30 min. Coefficients of non-photochemical, photochemical and dark fluorescence quenching (q_N, q_P and q_0) and the quantum yield of linear electron transport ($\Phi_{PS\,II}$; $(F'_m-F_t)/F'_m$) were analysed as summarized by von Willert *et al*. (1995). Rates of electron transport ($\mathcal{J}_F$) were estimated according to Krall & Edwards (1992) as

$$\mathcal{J}_F = \Phi_{PS\,II} \times PPFD \times a \times f. \quad (3)$$

The absorptivity a of the succulent leaves in the visible range was taken as 0·68 (Eller, Brinckmann & von Willert, 1983) and the light distribution factor between PS I and II, f, was set to 0·5 (Krall & Edwards, 1992).

Determination of malic acid concentrations

One h after illumination, and in the late afternoon, leaves were harvested and their perimeters traced on paper before weighing and drying to constant weight at 85 °C. Leaf water content was calculated from the difference between f. wt and d. wt and related to leaf surface. The projected leaf area was obtained from the paper traces with an area meter (Delta T Devices, Cambridge, UK). Malic acid concentration was determined enzymatically (Möllering, 1974) in hot water extracts.

RESULTS

In well watered LL plants mean net CO_2 uptake rates ($\mathcal{J}_{CO_2}$) were *c*. 50 % lower than in HL plants (Table 1). Nocturnal accumulation of malic acid (Δ-malate) tended to be higher (*c*. 50 %) in leaves of HL plants, which also appeared to be slightly larger, and had a higher specific leaf weight and tissue water content (Table 1).

Both at ambient oxygen concentration (21 %) and under non-photorespiratory conditions (2 % O_2), rates of dark respiration, net CO_2 uptake at saturating PPFD and the PPFD compensation point were higher in HL plants (Table 2). However, maximum apparent photon yield (i.e. initial slope of the PPFD dependence curves) and relative portion of photorespiration at saturating PPFD were nearly identical in plants of both treatments. Photosynthesis was saturated below 1000 μmol m^{-2} s^{-1} in the HL plants, and at < 550 μmol m^{-2} s^{-1} in LL plants. Exposing leaves to more than twice the saturating PPFD for *c*. 30 min did not lead to a reduction of $\mathcal{J}_{CO_2}$, i.e. there were no signs of photoinhibition, regardless of the O_2 concentration used (Fig. 1*a*, *b*).

At 2 % O_2, carboxylation efficiency (the initial slope of the plot of net carbon exchange vs. the internal CO_2 mole fraction) was nearly identical to values determined at ambient O_2 when measured at 640 μmol m^{-2} s^{-1} and at saturating PPFD in HL plants (Fig. 2*a*). At 21 % O_2, carboxylation efficiency increased with PPFD from 0·016 at 280 μmol m^{-2} s^{-1} to 0·022 at saturating PPFD, while the CO_2 compensation point Γ decreased from 64 to 50 μmol mol^{-1}. Maximum PPFD and CO_2 saturated $\mathcal{J}_{CO_2}$ were *c*. 4·7 and 6·9 μmol m^{-2} s^{-1} (at 21 % and 2 % O_2, respectively) as extrapolated using a quadratic function.

From the regression analysis of PPFD response curves at low PPFD ('Kok effect', cf. Villar, Held & Merino, 1994) it was estimated that mitochondrial respiration retained *c*. 50 % of its activity during illumination (Table 2). 'Day respiration' at higher PPFD could be analysed by the close inspection of net CO_2 exchange response to low levels of c_i, measured at different PPFD ('Laisk'-method; cf. Villar *et al*., 1994). The point where the initial slopes of these plots intersect (Fig. 2*b*) gives an estimate of both R_d and Γ_*. At PPFD < 280 μmol m^{-2} s^{-1} residual mitochondrial respiration activity was *c*. 40 % (0·46 μmol m^{-2} s^{-1}) and Γ_* was *c*. 31 μmol mol^{-1}.

The rates of electron flow required to satisfy carboxylation and oxygenation ($\mathcal{J}_{CO}$) were *c*. 40 and 38 % of total linear photosynthetic electron transport rates ($\mathcal{J}_F$) near or at saturating PPFD in HL and LL plants (Fig. 3*a*, *b*). The theoretical minimum electron flow used for carbon assimilation ($\mathcal{J}_{Cm}$), was *c*. 25 % of the total photosynthetic electron flow in plants of both treatments (Fig. 3*a*, *b*). Furthermore, electron flow rates that should additionally meet total ATP consumption of C_3 photosynthesis ($\mathcal{J}_{CA}$) were 48 % and 45 % of $\mathcal{J}_F$ at higher PPFD (Fig. 3*a*, *b*). This is further substantiated by a plot of $\mathcal{J}_F$ vs. $\mathcal{J}_{CA}$ (Fig. 4). Although

Table 1. *Effects of PPFD during growth on leaf surface area, specific leaf weight, water content on a leaf surface area basis and on nocturnal accumulation of malic acid* (Δ-*malate*)

Parameter	PPFD (μmol m^{-2} s^{-1})	
	220	550
Leaf surface area (cm^2)	5·21 ± 1·82	6·58 ± 1·53
Specific leaf weight (kg$_{DW}$ m^{-2})	0·0263 ± 0·0144	0·0356 ± 0·0125
Leaf surface based water content (g$_{H_2O}$ dm^{-2})	7·86 ± 1·87	9·45 ± 2·00
Mean daytime CO_2 uptake rates (μmol m^{-2} s^{-1})	1·22 ± 0·14	2·51 ± 0·31
Δ-malate (mmol m^{-2})	4·11 ± 1·17	6·06 ± 1·11

Water content on a leaf surface area basis is given in [g$_{H_2O}$ dm^{-2}] to allow easy comparison with values of the degree of succulence often used in the literature. Data are means ± SD. Day/night environmental conditions were: T 25/15 °C; r.h. 40/85 %.

Table 2. *Photon flux density-dependence characteristics of photosynthesis as influenced by PPFD during growth*

Parameter	PPFD during growth (μmol m^{-2} s^{-1})			
	220		550	
	21 % O_2	2 % O_2	21 % O_2	2 % O_2
Dark respiration (μmol m^{-2} s^{-1})	0·32 ± 0·02	0·16 ± 0·06	1·15 ± 0·03	0·84 ± 0·05
Light compensation point (μmol mol^{-1})	20 ± 3	7 ± 3	78 ± 14	33 ± 4
Apparent photon yield of CO_2 fixation	0·028 ± 0·004	0·035 ± 0·001	0·035 ± 0·003	0·052 ± 0·003
Light saturated J_{CO_2} (μmol m^{-2} s^{-1})	1·39 ± 0·13	2·55 ± 0·40	2·98 ± 0·08	5·57 ± 0·11
Photorespiration (%)	45		46	

Measurements were performed under photorespiratory (21 % O_2) and non-photorespiratory conditions (2 % O_2) to allow estimation of photorespiratory activity, given as the percentage of reduction of maximum photosynthetic CO_2 fixation at 2 % O_2.

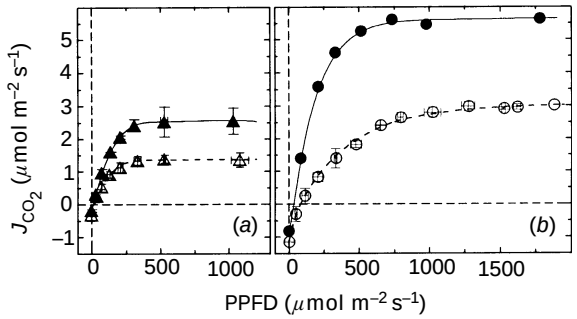

Figure 1. Photon flux density responses of net CO_2 exchange, measured under photorespiratory (21 % O_2; dotted lines, open symbols) and non-photorespiratory (2 % O_2; solid lines, closed symbols) conditions (leaf temperature = 25 °C, dew point = 12 °C) in LL (*a*) and HL plants (*b*).

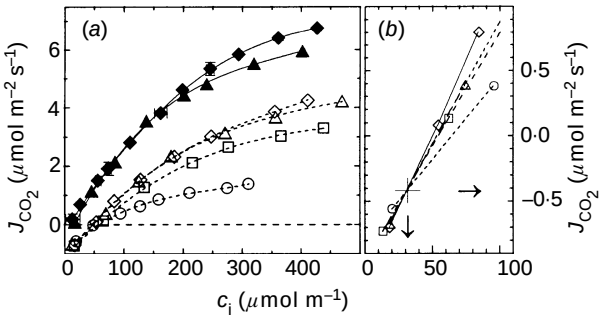

Figure 2. (*a*) Net CO_2 exchange ($\mathcal{J}_{CO_2}$) as a function of internal CO_2 mole (c_i) fraction of high-light-grown plants. Measurements were performed under non-photorespiratory (2 % O_2, closed symbols) and photorespiratory (21 % O_2, open symbols) conditions (leaf temperature = 25 °C, dew point = 12 °C) at PPFD of either 280 (○), 520 (□), 640 (△) or 1100 μmol m^{-2} s^{-1} (◇). The point where the initial slopes of the plots $\mathcal{J}_{CO2}$ vs. c_i (measured at 21 % O_2) intersect is shown in (*b*). The horizontal arrow indicates the rate of day respiration (R_d), the photocompensation point (Γ_*) is denoted by the vertical arrow.

$\mathcal{J}_{Cm}$ was much lower, it was linearly related (r^2 = 0·972) to total electron flow (Fig. 4) and was independent of PPFD during growth.

LL and HL plants differed distinctly in their responses to increasing PPFD. Non-photochemical fluorescence quenching, q_N, saturated at relatively low PPFD in LL plants (Fig. 5*a*). Nevertheless, maximum values of $q_N$were similar for plants of both treatments (0·701 ± 0·073 and 0·771 ± 0·025 for LL and HL plants, respectively). Similar responses were displayed by the quenching of the initial fluorescence, q_0 (Fig. 5*b*). Although photochemical quenching, q_P, declined linearly with increasing PPFD in HL individuals (Fig. 5*c*), it declined rapidly in LL plants when PPFD exceeded flux densities experienced during growth. Furthermore,

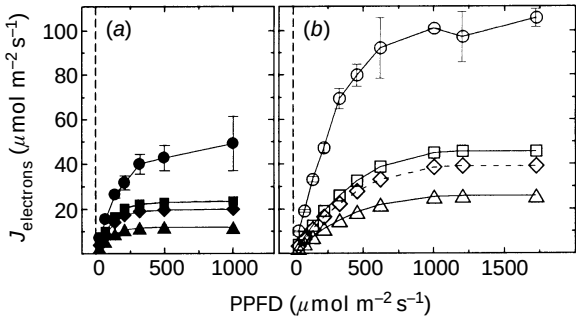

Figure 3. Rates of linear electron flow ($\mathcal{J}_{electrons}$) in LL (*a*) and HL plants (*b*). Data were either obtained from fluorescence analysis (○) or calculated from gas exchange measurements as the electron flow rates to satisfy total ATP consumption, $\mathcal{J}_{CA}$, (□), gross carbon fixation, $\mathcal{J}_{CO}$, (◇) or minimum rates to CO_2 fixation, $\mathcal{J}_{Cm}$, (△).

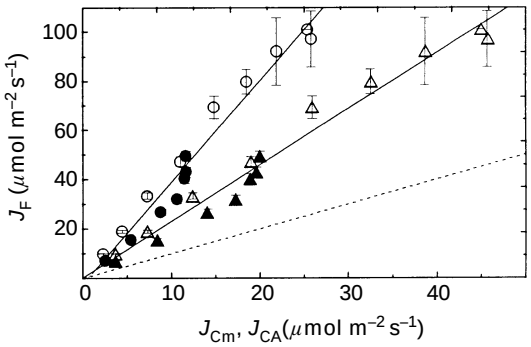

Figure 4. Correlation between $\mathcal{J}_{Cm}$ (○), or $\mathcal{J}_{CA}$ (△), respectively and linear photosynthetic electron transport through PS II ($\mathcal{J}_F$), calculated from fluorescence measurements, with linear regression analyses (solid lines). The former relation yielded a coefficient of determination of 0·972, and the latter yielded 0·966. The dotted line indicates the 1:1 ratio. Data were obtained from PPFD dependence curves, determined with LL (filled symbols) and HL plants (open symbols). Temperature during measurements was 25 ± 1 °C.

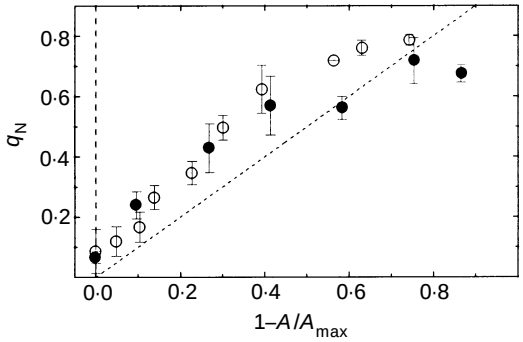

Figure 6. Correlation between non-photochemical quenching, q_N, and the relative amount of photons not being utilized by photochemistry, computed as $(1-A/A_{max})$ in LL (●) and HL (○) individuals. The dashed line indicates the 1:1 relationship.

q_P was lower at saturating PPFD, and quantum yield of linear electron transport (Φ_{PSII}) was significantly smaller in these plants at each PPFD (Fig. 5*d*).

The relative amount of photons not being utilized by photochemistry can be calculated as $(1-A/A_{max})$ (Schreiber & Bilger, 1987). A_{max}, the corresponding hypothetical maximum assimilation rate, occurring if there were no limitation to photosynthesis, could be computed from the product of apparent maximum photon yield of CO_2 fixation and the prevailing PPFD. Total q_N increased linearly as photosynthetic energy conversion capacity was progressively exceeded (Fig. 6), but maximum q_N values were attained when $(1-A/A_{max})$ was 0·7. The resulting deviation from linearity was more pronounced in LL plants.

DISCUSSION

Delosperma tradescantioides effectively adapts to the ambient PPFD, because the plants derived from the same stock adjusted to the given growth PPFD.

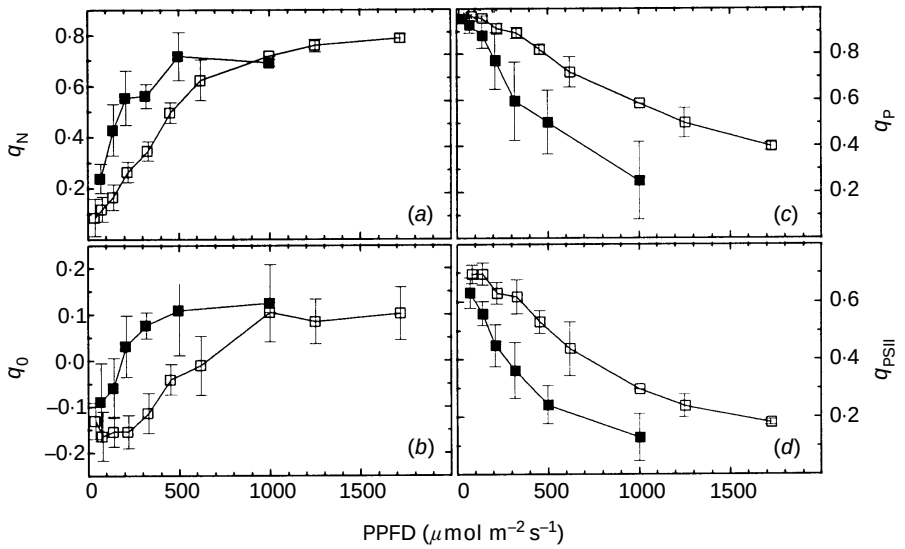

Figure 5. Non-photochemical (q_N) (*a*), dark fluorescence (q_0) (*b*), photochemical quenching (q_P) (*c*), and photon yield of linear electron transport through PS II ($\Phi_{PS\,II}$) (*d*), as a function of PPFD in low-(■) and high-(□) light-grown plants.

Leaf morphology displayed several features attributed to shade vs. sun plant acclimation found in CAM plants (Adams, Osmond & Sharkey, 1987; Fetene *et al.*, 1990), although the observed differences in leaf size, specific leaf weight or water content were only small. PPFD-dependent differences in photosynthetic performance were, however, striking. HL plants showed many features attributed to sun plants (Lüttge *et al.*, 1986), e.g. large rates of dark respiration, and high points of PPFD compensation and saturation. PPFD-saturated CO_2 uptake was also much higher than in LL plants, a commonly observed pattern (Herppich, 1997; Midgley *et al.*, 1992). However, apparent quantum yield of CO_2 uptake was enhanced in HL plants, a characteristic normally (Borland & Griffiths, 1990; Lüttge *et al.*, 1991), but not always (Fetene *et al.*, 1990), found in LL plants. *D. tradescantioides* may thus be seen as a heliophilic CAM plant which displays some shade tolerance. It appears to be well adapted to open, exposed habitats, as also found for *Talinum triangulare* which inhabits comparable sites in the field (Herrera, Delgado & Paraguatey, 1991).

Ambient air photosynthetic capacity (LL: 1·6 μmol m^{-2} s^{-1}; HL: 3·2 μmol m^{-2} s^{-1}) was relatively high in *D. tradescantioides*. Lüttge *et al.* (1986) reported a range of PPFD-saturated $\mathcal{J}_{CO_2}$ of 0·6–4·2 μmol m^{-2} s^{-1} for several epiphytic CAM plants, whereas it did not exceed 3·2 μmol m^{-2} s^{-1} in four CAM species of the genus *Plectranthus* (Herppich & Herppich, 1996). By contrast, in some species of the genus *Kalanchoë* PPFD and CO_2 saturated photosynthesis can be > 16 μmol m^{-2} s^{-1} (Adams *et al.*, 1987; Lüttge *et al.*, 1991), recalculated on a leaf surface basis.

Regardless of growth conditions, photosynthetic CO_2 uptake was substantially enhanced at low O_2, indicating a high degree (*c.* 45 %) of photorespiration at ambient CO_2 concentration. Photorespiration in C_3 plants is normally in the range 25–40 % (at 25 °C; Edwards & Walker, 1983). Consequently, CAM-cycling could not enhance photosynthetic competence in *D. tradescantioides* under photorespiratory conditions. Even during the early part of the day decarboxylation of the small amounts of nocturnally accumulated malic acid did not effectively increase c_i (Herppich *et al.*, 1996), which otherwise would have reduced photorespiration. These results substantiate the opinion that CAM cycling might not necessarily be an efficient mechanism for conservation of water and carbon (Martin, 1996).

The range of values of 'day respiration' determined in *D. tradescantioides* corresponded well with previous reports for several C_3 plants (Brooks & Farquhar, 1985; Villar *et al.*, 1994). Results also indicate that R_d declined with increasing PPFD (Brooks & Farquhar, 1985). Γ_* was slightly lower in *D. tradescantioides* (*c.* 30 μmol mol^{-1}) than in C_3 plants (ranging between 35 and 42 μmol mol^{-1} at 25 °C, Brooks & Farquhar (1985); Villar *et al.* (1994)), but broadly supports the notion that kinetic properties of Rubisco are independent of the carbon metabolism of the plants.

The fact that total linear photosynthetic electron transport rates ($\mathcal{J}_F$) were larger than those that should additionally meet total ATP consumption of C_3 photosynthesis ($\mathcal{J}_{CA}$) might indicate that additional electron sinks became increasingly important mainly at high PPFD (e.g. the Mehler reaction, ascorbate regeneration, the malate valve or nitrate assimilation; Heber, Neimanis & Kaiser (1996*a*); Osmond, Popp & Robinson (1996)). However, these mechanisms might not be of great importance in well watered plants (Heber *et al.*, 1996*b*). On the other hand, CO_2-saturated rates of photosynthetic O_2 evolution (i.e. photosynthetic capacity) might be much higher than maximum rates of ambient air CO_2 uptake under similar conditions in well watered CAM plants (e.g. Adams & Osmond, 1988; Maxwell *et al.*, 1994). Thus, the observed discrepancy might be due to the higher ATP and $NADPH/H^+$ requirement of CAM plants during malic acid decarboxylation and regeneration of storage carbohydrate (Winter & Smith, 1996). Since measurements were mostly performed in the late light phase this could also indicate a large degree of 'futile carbon cycling' (Osmond *et al.*, 1996) via phosphoenolpyruvate carboxylase and Rubisco active at the same time in *D. tradescantioides*. Thus, CAM cycling might act as a photoprotective process in *D. tradescantioides* in that it allows dissipation of excessive ATP and reductant (Roberts *et al.*, 1996). Interestingly, maximum levels of $\mathcal{J}_F$ obtained in species of the genus *Clusia* early in the day were nearly double the theoretical minimum electron flow used for carbon assimilation ($\mathcal{J}_{Cm}$, estimated from data of Roberts *et al.* (1996)).

The fact that $\mathcal{J}_F$ closely matches changes in $\mathcal{J}_{CA}$ and $\mathcal{J}_{Cm}$ suggests that energy gain and energy use were tightly co-regulated in *D. tradescantioides*, i.e. 'photosynthetic control' (Foyer *et al.*, 1990) functioned remarkably well even at high PPFD. Actual quantum yield of PS II, $\Phi_{PS\,II}$, was reduced at much lower PPFD in LL plants. This was mainly due to the fast rising q_N (a relative measure of radiationless, thermal energy dissipation), at least at non-saturating PPFD. The plot of q_N vs. the fraction of excessively absorbed photons revealed that the capacity of the photosynthetic apparatus to dissipate excessive PPFD was well adapted to the prevailing photosynthetic efficiency in plants of both treatments. This agrees with findings of Demmig & Winter (1988) who showed that there was a high similarity in this relationship among several C_3 species regardless of growth PPFD or nutrient conditions during growth. However, in the present investigation the capacity of the mechanism(s)

comprising q_N, appeared to be exhausted when the relative amount of excitation energy not utilizable by photochemistry exceeded 0·7. Nevertheless, during the short-term exposure used for both gas exchange and fluorescence measurements even at the highest PPFD no indications of photoinhibition could be found. Besides the proposed futile carbon cycling, in ambient air this might also result from the high degree of photorespiration which is assumed to protect the photosynthetic apparatus against photoinactivation (Heber *et al*., 1996*b*). The large differences between $\mathcal{J}_{Cm}$ and $\mathcal{J}_{CO}$ denote high rates of photorespiration in *D. tradescantioides*, as their ratio closely matches that obtained from gas exchange measurements at 21 and 2 % O_2.

In conclusion, flexibility in photosynthetic characteristics displayed by *D. tradescantioides* extends to its PPFD response characteristics. *D. tradescantioides* is a heliophilic, partly shade tolerant species that adapts photosynthetically to a range of ambient PPFD. Although photorespiratory activity appears high, plants did not suffer large decreases in net carbon uptake at higher temperature. No evidence for photoinhibition could be found, even under non-photorespiratory conditions. Thus, the photosynthetic machinery appears well buffered against excessive energy absorption regardless of the range of light experienced during growth. Furthermore, the presented results lead to the assumption that the ecological function of CAM cycling might be that of a photoprotective mechanism.

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