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Susceptibility of green leaves and green flower petals of CAM orchid *Dendrobium* cv. Burana Jade to high irradiance under natural tropical conditions

J. HE* and L.C.D. TEO

Natural Sciences and Science Education Academic Group, National Institute of Education,
Nanyang Technological University, 1 Nanyang Walk, Singapore 637 616

Abstract

Photosynthetic rates of green leaves (GL) and green flower petals (GFP) of the CAM plant *Dendrobium* cv. Burana Jade and their sensitivities to different growth irradiances were studied in shade-grown plants over a period of 4 weeks. Maximal photosynthetic O_2 evolution rates and CAM acidities [dawn/dusk fluctuations in titratable acidity] were higher in leaves exposed to intermediate sunlight [a maximal photosynthetic photon flux density (PPFD) of 500–600 μmol m^{-2} s^{-1}] than in leaves grown under full sunlight (a maximal PPFD of 1 000–1 200 μmol m^{-2} s^{-1}) and shade (a maximal PPFD of 200–250 μmol m^{-2} s^{-1}). However, these two parameters of GFP were highest in plants grown under the shade and lowest in full sun-grown plants. Both GL and GFP of plants exposed to full sunlight had lower predawn F_v/F_m [dark adapted ratio of variable to maximal fluorescence (the maximal photosystem 2 yield without actinic irradiation)] than those of shade-grown plants. When exposed to intermediate sunlight, however, there were no significant changes in predawn F_v/F_m in GL whereas a significant decrease in predawn F_v/F_m was found in GFP of the same plant. GFP exposed to full sunlight exhibited a greater decrease in predawn F_v/F_m compared to those exposed to intermediate sunlight. The patterns of changes in total chlorophyll (Chl) content of GL and GFP were similar to those of F_v/F_m. Although midday F_v/F_m fluctuated with prevailing irradiance, changes of midday F_v/F_m after exposure to different growth irradiances were similar to those of predawn F_v/F_m in both GL and GFP. The decreases in predawn and midday F_v/F_m were much more pronounced in GFP than in GL under full sunlight, indicating greater sensitivity in GFP to high irradiance (HI). In the laboratory, electron transport rate and photochemical and non-photochemical quenching of Chl fluorescence were also determined under different irradiances. All results indicated that GFP are more susceptible to HI than GL. Although the GFP of *Dendrobium* cv. Burana Jade require a lower amount of radiant energy for photosynthesis and this plant is usually grown in the shade, is not necessarily a shade plant.

Additional key words: CAM acidity; chlorophyll; electron transport rate; fluorescence induction; photosynthetic O_2 evolution; photosynthetic photon flux density; quenching.

Introduction

In tropical orchid, several factors influence the response of leaf photosynthesis to irradiation. First, supra-optimal leaf temperatures that accompany high irradiance (HI) cause reduction in photosynthesis (He *et al.* 1998). Second, virus infection enhances decrease of photosynthesis (He *et al.* 2004). Providing higher growth irradiance under well-watered and well-supplied mineral nutrients environment is one way of enhancing the harvestable yield in the tropical orchid (Hew and Yong 1994, 1997). Increasing the photosynthetic rate of source leaves

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*Corresponding author; fax: 65-68969432, e-mail: jie.he@nie.edu.sg

Abbreviations: Chl – chlorophyll; DM – dry matter; ETR – electron transport rate; F_0 – minimal fluorescence yield of a "dark-adapted" sample; F_0' – modulated fluorescence during brief interruption of actinic irradiation in the presence of far-red irradiation; F_m and F_v – maximal and variable fluorescence yields obtained from a dark-adapted sample upon application of a saturating pulse of radiation, respectively; F_m' – maximal fluorescence yield at any given time under irradiation; F_s – Chl fluorescence yield during irradiation; GFP – green flower petal; GL – green leaf; HI – high irradiance; PPFD – photosynthetic photon flux density; PS2 – photosystem 2; q_N – non-photochemical quenching of Chl fluorescence; q_P – photochemical quenching of Chl fluorescence; TA – titratable acidity.

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by increasing irradiance is, however, not feasible because many tropical orchids are shade plants (Hew and Yong 1994) and are virus-infected (He *et al.* 2004). Photosystem 2 (PS2), an intricate thylakoid membrane complex with a light-driven water-plastoquinone-oxidoreductase activity, is the primary target of this phenomenon, which is known as photoinhibition (Osmond 1994). HI may lead to photoinhibition of the leaves in plants grown under tropical natural conditions (He *et al.* 1996) including orchid plants (He *et al.* 1998, 2004). When plants are exposed to excess photons, different mechanisms operate to protect the photosynthetic apparatus from 'over-energization'. Photoinhibition is evident at the leaf level as a reduction in quantum yield and maximal photosynthetic capacity (Björkman and Demmig 1987, Osmond 1994). Another useful indicator of photoinhibition is Chl fluorescence (Björkman and Demmig 1987). Photoinhibited leaves exhibiting a decline in quantum yield of O_2 evolution and maximal photosynthetic rate per leaf area also have a corresponding decrease in F_v/F_m in plants grown under natural tropical conditions (He *et al.* 1996, 2004). Differentiation of the allocation of excitation energy to photochemistry or radiation-less dissipation processes can be determined *via* measurements of photochemical (q_P) and non-photochemical fluorescence quenching (q_N) together with determination of O_2 evolution (Weis *et al.* 1987, Demmig and Winter 1988). The mechanism of q_N, associated with thermal dissipation of excitation energy may play an important role in photoprotection (Chow 1994). An increased q_N is believed to protect the photochemical apparatus against the destructive effects of excess photon energy (Weis *et al.* 1987). When there is an imbalance between the photon energy absorbed by a photosynthetic organism and that which can be utilized in photosynthesis, photo-oxidative stress can occur. Therefore, the breakdown of Chl resulting from photo-oxidative damage may also be associated with the reduction in photosynthetic capacity induced by HI (Lichtenthaler *et al.* 1981, He *et al.* 1996).

Johnson (1993) reported that both a drop in CO_2 gas exchange and leaf chlorosis indicate photoinhibition in the orchid, *Deceoclades masculata*, when exposed to sudden or drastic increase in photosynthetic photon flux densities (PPFD). The efficiency of energy utilisation by PS2 in *Petunia* corolla was also lower than in green leaves (GL; Weiss *et al.* 1988). Khoo *et al.* (1997) and He *et al.* (1998) found that colourful flower petals of *Dendrobium* cv. Sonia were capable of photosynthesizing although their photosynthetic rates per leaf area were much lower than those of their GL. They also found that the utilisation of photon energy was much higher in leaves of *Dendrobium* cv. Sonia as compared to that of colourful flower petals of the same plants. Many tropical orchids have green flower petals (GFP) and they are popular potted or cut orchid flowers in Singapore. For instance, the CAM orchid *Dendrobium* cv. Burana Jade gained its popularity due to its green jade look of flower petals. Since HI damages both GL and GFP, many orchids including cv. Burana Jade are planted under shade in commercial systems. Nonetheless, plants grown under low irradiance may also experience a reduction in the photosynthetic rate, resulting in a decline in growth rate (He *et al.* 1998, 2004). Under natural tropical conditions, HI not only saturates photosynthesis of orchid leaves but also subjects the exposed green inflorescence to HI-stress. The response of GFP to HI and the utilisation of photon energy by GFP have not been characterized. We grew the cv. Burana Jade orchid plants under different irradiances to study the photosynthetic capacities and utilisation of photon energy of both GL and GFP. The results may be useful for the local orchid growers on how to increase the photosynthetic capacities of source leaves and at the same time, protect the GFP from HI-stress.

Materials and methods

Plants: Mature plants of *Dendrobium* cv. Burana Jade (*Dendrobium* Madame Uraiwan × *Dendrobium* May Neal), a CAM orchid with 3–4 full newly opened inflorescences, were obtained from a commercial nursery. These plants were normally grown in shade, under which the maximum midday PPFD was 200–250 μmol m^{-2} s^{-1} in the commercial nursery. After purchasing from the nursery, these plants were acclimated for two weeks in the orchid garden at National Institute of Education, Singapore under a similar shade condition, before transferring them to different growth irradiances for irradiation treatments. The daily ambient temperature ranged from 24 to 34 °C. All plants were watered twice a day. They were fertilised (N : P : K ratio of 1 : 1 : 1) and sprayed with fungicide once a week. Flag leaves and GFP of number 4 and 5 (from the top) were used for the different measurements.

Intermediate and full sunlight treatment: To study the effect of different growth irradiance plants grown in pots under shade were transferred to full and intermediate sunlight. Maximum PPFDs of full and intermediate sunlight during midday were 1 000–1 200 and 500–600 μmol m^{-2} s^{-1}, respectively, in the orchid garden. Some plants were maintained under shade with midday PPFD of 200–250 μmol m^{-2} s^{-1} to serve as control. Reduced growth irradiances were achieved by covering the plants with one and two layers of netting for intermediate sunlight and shade, respectively. The daily ambient temperature ranged from 24 to 34 °C. During the period of irradiation, all plants were watered twice a day. They were also fertilised and sprayed with fungicide once week.

Measurement of photosynthetic O_2 evolution on detached GL and GFP: The maximal photosynthetic O_2

evolution (P_{max}) of leaves and GFP were determined using a leaf disc O_2 electrode (*Hansatech*, King's Lynn, Norfolk, UK), under PPFD of 1 000 µmol m^{-2} s^{-1} at 25 °C using GL sections and GFP sections in saturating CO_2 condition (1 % CO_2 from a 1 M carbonate/bicarbonate buffer, pH 9) as described by Ball *et al.* (1987).

Titratable acidity (CAM acidity; TA) of flag GL and GFP (number 4 and 5 from the top of inflorescence) was determined at both 09:00 and 18:00 h. Five discs (7 mm diameter) were punched out of each plant sample, with a cork borer, and transferred into heat-tolerant test tubes containing 1 cm^3 of distilled water (neutral pH). The tubes were then immersed into a boiling water-bath on a hot plate and left for 15 min. After which, the tubes were allowed to cool to room temperature. The extract was subsequently titrated against 0.01 M sodium hydroxide solution, NaOH(aq), using three drops of phenolphthalein as indicator until the end-point (pink colouration) was reached. The volume of NaOH(aq) needed to reach the end-point of titration was recorded. The plant materials were wrapped in aluminium foil and kept at 80 °C until a constant matter was obtained [dry matter (DM)]. TA was calculated using the formula TA = (0.01× volume)/DM. The dawn/dusk fluctuation of TA was calculated from the difference between TA at 09:00 and 18:00 h.

Measurements of F_v/F_m under natural conditions were made with Chl fluorometer (Plant Efficiency Analyser, PEA, *Hansatech Instruments*, England). The leaves were pre-darkened with clips for 15 min prior to measurements. Dark-adapted leaves were then placed under the light pipe and irradiated with the pulsed low intensity-measuring beam to measure F_0, initial minimal Chl fluorescence. F_m, maximum Chl fluorescence, was assessed by a 0.8-s saturated pulse (>3 000 µmol m^{-2} s^{-1}). The variable fluorescence yield, F_v, was determined as $F_m - F_0$. The efficiency of excitation energy captured by open PS2 reaction centres in dark-adapted plant samples was estimated by the F_v/F_m. All predawn and midday, F_v/F_m was measured on the same spots of intact GL and GFP throughout the treatment period, respectively, between 07:00–07:30 and 12:00–13:00 h local time.

Measurements of q_P, q_N, and ETR in the laboratory were made using a modulated fluorescence system (*PAM-2000*, *Walz*, Effeltrich, Germany) on detached GL and GFP, freshly harvested at 10:00 h. Fluorescence quenching of the dark-adapted GL and GFP was measured using the saturating pulse method. After a 30-min dark adaptation, the minimum (dark) fluorescence yield (F_0) was obtained upon excitation of GL and GFP with a weak measuring beam from a light-emitting diode. The maximum fluorescence yield (F_m) was determined with 600 ms saturating pulse of "white light" (6 000 µmol m^{-2} s^{-1}). Variable fluorescence (F_v) was calculated as $F_m - F_0$. The leaf was then allowed to adapt to 10 successive irradiances (5-min irradiation at 13 to 2 526 µmol m^{-2} s^{-1} at 25 °C). At the end of each irradiation period, a saturating pulse was fired to measure the maximum fluorescence yield during actinic irradiation (F_m'), and the Chl fluorescence yield during actinic irradiation (F_s) was recorded before every saturation pulse. The level of modulated fluorescence during a brief interruption (3 s) of actinic irradiation in the presence of 6 µmol m^{-2} s^{-1} far red (730 nm) radiation (F_0') was also recorded. Quenching due to non-photochemical dissipation of absorbed photon energy (q_N) was calculated at the end of each irradiation period, according to the equation $q_N = (F_m - F_m')/(F_m - F_0')$ (van Kooten and Snel 1990). The coefficient for photochemical quenching, q_P, represents the fraction of open PS2 reaction centres and was calculated as $(F_m' - F_s)/(F_m' - F_0')$ (Schreiber *et al.* 1986). The steady state-modulated Chl fluorescence, $\Delta F/F_m'$ was calculated as ($\Delta F/F_m' = F_m' - F_s/F_m'$). Electron transport rate (ETR) was calculated as ETR = PPFD×$\Delta F/F_m'$×0.5×0.84 (Rascher *et al.* 2000).

Chl SPAD reading: Non-destructive Chl readings were made using a handheld Chl meter (*SPAD-502*, *Minolta*, Japan). The total Chl readings were taken on the same spots of GL and GFP on which the predawn and midday F_v/F_m were recorded.

Measurement of Chl content: 0.05 g of each GL and GFP sample was weighed and cut into smaller pieces. Chl was extracted from these samples using dimethyl-formamide, and quantified spectrophotometrically at wavelengths of 647 and 664 nm (Wellburn 1994).

Statistical analysis: Data from each experimental treatment were assessed using One Way ANOVA on *MINITAB* (*MINITAB*, release 14 December, 2004).

Results

***P_{max}* and CAM acidity (TA)**: After exposure to different irradiations for 4 weeks, P_{max} and TA of GL and GFP were determined (Fig. 1). The highest P_{max} was obtained with GL of plants transferred from shade to intermediate sunlight, followed by those control plants grown under shade conditions over the same period of 4 weeks. Leaves of plants transferred from shade to full sunlight had a lowest P_{max} (Fig. 1*A*). There were significant differences in P_{max} between control shade plants and those transferred from shade to intermediate sunlight ($p<0.05$) and to full sunlight ($p<0.05$). GFP were unable to photosynthesize at rates compatible with GL (Fig. 1*A*). The highest P_{max} of GFP was obtained from control shade-grown plants, followed by those transferred from shade to intermediate sunlight. GFP transferred from shade to full sunlight exhibited a greatest reduction in P_{max} (Fig. 1*A*). There

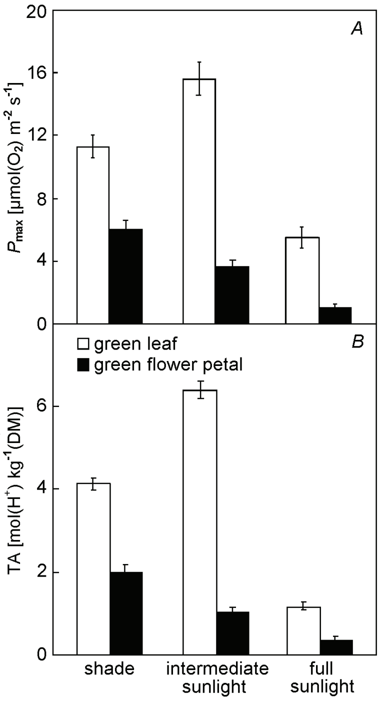

Fig. 1. Maximum photosynthetic rate, P_{max} (*A*) and CAM activity (*B*) of *Dendrobium* cv. Burana Jade green leaves (GL) and green flower petals (GFP) grown under shade or intermediate and full sunlight during 4 weeks. Means of 4 measurements from 4 different GL and 4 different GFP. *Vertical bars* represent standard errors.

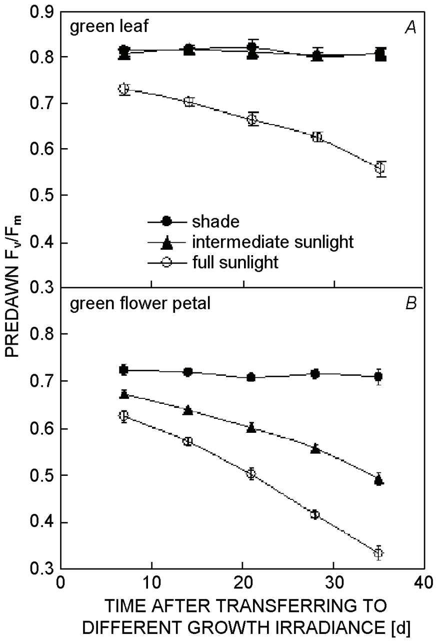

Fig. 2. Changes in predawn F_v/F_m of green leaves, GL (*A*) and green flower petals, GFP (*B*) of *Dendrobium* cv. Burana Jade grown under shade, intermediate, and full sunlight for a period of 35 d. Means of 12 measurements for F_v/F_m obtained on various days of the experiment, from 12 different GL and 12 different GFP. *Vertical bars* represent standard errors.

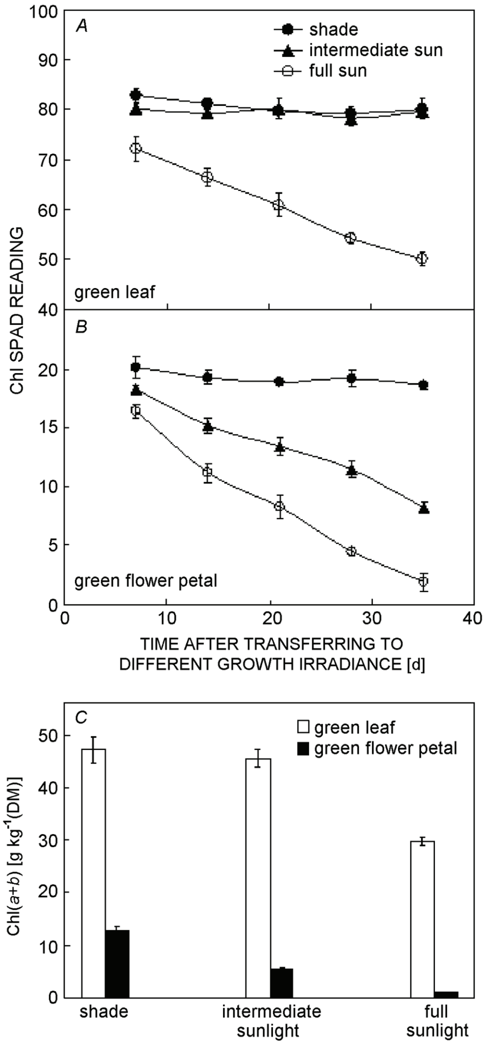

Fig. 3. Changes in chlorophyll (Chl) SPAD readings (*A, B*) and Chl content (*C*) of green leaves (GL) and green flower petals (GFP) of *Dendrobium* cv. Burana Jade grown under shade, intermediate, and full sunlight. Means of 12 measurements from 6 different GL and 6 different GFP. *Vertical bars* represent standard errors.

was a significant difference in P_{max} in GFP of control shade plants and those transferred to intermediate sunlight and to full sunlight for 4 weeks ($p<0.05$). The differences in CAM acidities (dawn/dusk fluctuations in TA) among the different GL and GFP were similar to those of P_{max} (Fig. 1*B*).

F_v/F_m and Chl content: Changes in predawn F_v/F_m and Chl content of GL and GFP grown in shade after exposure to intermediate and full sunlight for a period of 35 d are shown in Figs. 2 and 3, respectively. GL exposed to intermediate sunlight for 35 d did not show significant differences in predawn F_v/F_m from those of control shade plants (Fig. 2*A*). Compared to control shade-grown plants, a significant decrease in predawn F_v/F_m in GL exposed to full sunlight was observed from the first measurement, that was, one week after exposure to full sunlight ($p<0.05$). There were significant decreases in predawn F_v/F_m of GFP exposed both to intermediate and to full sunlight compared to those of GFP of control shade plants ($p<0.05$, Fig. 2*B*). The reduction in predawn F_v/F_m of GFP exposed to full sunlight was much pronounced. Similar trends were observed in Chl SPAD readings recorded from the same spots of GL (Fig. 3*A*) and GFP (Fig. 3*B*). Destructive Chl measurements made 35 d after different irradiations also showed similar results (Fig. 3*C*). Although they fluctuated with prevailing irradiance, changes in midday F_v/F_m of GL (Fig. 4*B*) and GFP (Fig. 4*C*) after exposure to different growth irradiances (Fig. 4*A*) were similar to those of predawn F_v/F_m (Fig. 2). For instance, on the last day (*i.e.* day 35) of irradiation, when it was a sunny day with a maximal midday PPFD of 1 125 μmol m^{-2} s^{-1} (Fig. 4*A*) under full sunlight, the midday F_v/F_m values were 0.441(Fig. 4*B*) and 0.222 (Fig. 4*C*), respectively, for GL and GFP. These values indicate that the decreases in midday F_v/F_m were much more pronounced in GFP than in GL under full sunlight.

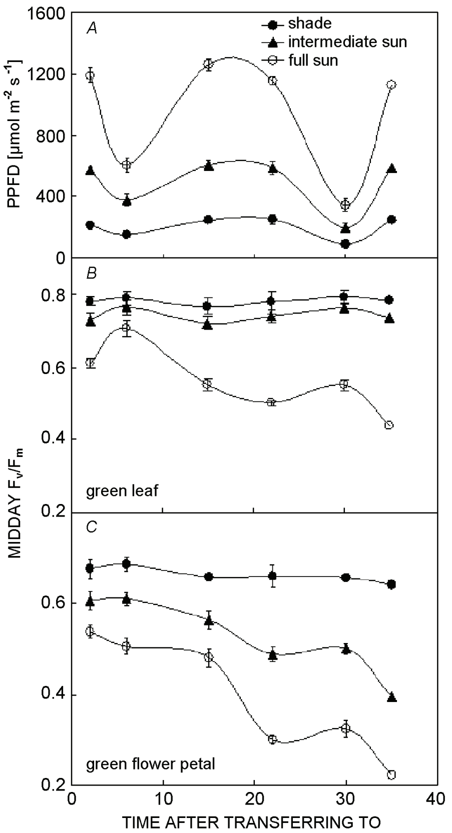

Fig. 4. Changes in midday photosynthetic photon flux density (PPFD) (*A*) and midday F_v/F_m of green leaves, GL (*B*) and green flower petals, GFP (*C*) of *Dendrobium* cv. Burana Jade grown under shade, intermediate, and full sunlight for a period of 35 d. (*B, C*) means of 12 measurements from 12 different GL and 12 different GFP. *Vertical bars* represent standard errors.

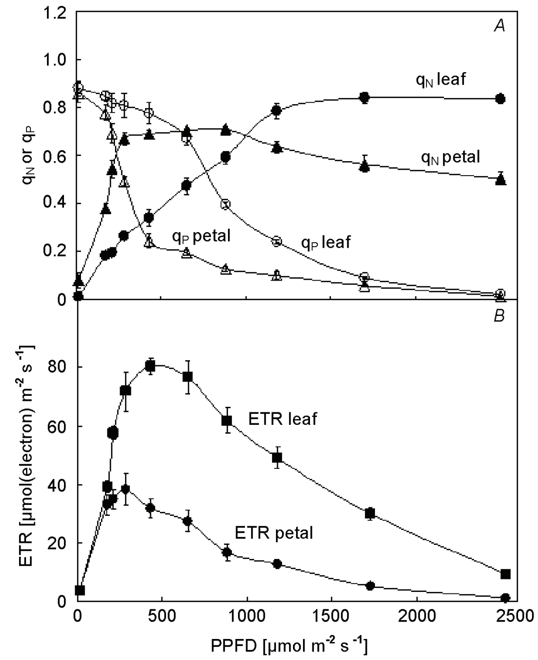

Fig. 5. Changes in q_N and q_P (*A*) and ETR (*B*) of detached green leaves, GL and green flower petals, GFP of *Dendrobium* cv. Burana Jade under different photosynthetic photon flux densities (PPFDs). Means of 6 measurements from 6 different GL and 6 different GFP. *Vertical bars* represent standard errors.

Chl fluorescence parameters, q_P, q_N, and ETR measured under different irradiances in laboratory: These parameters were used to explore the utilisation of photon energy by GL and GFP. q_P of GL was consistently high with values of 0.88–0.78 under PPFD of 13–430 μmol m^{-2} s^{-1}. A sharp decrease of q_P in GL was observed when PPFD was higher than 665 μmol m^{-2} s^{-1} with its values less than 0.1 and almost zero, respectively, under PPFD of 1 700 and 2 500 μmol m^{-2} s^{-1} (Fig. 5*A*). There was a gradual increase in q_N of leaves from PPFD of 13–880 μmol m^{-2} s^{-1} after which it formed plateau at around 0.8 (Fig. 5*A*). GFP exhibited similar trends for q_P and q_N values as GL. However, the decrease of q_P with increasing of PPFD occurred at much lower PPFDs than that of GL (Fig. 5*B*). The increase of q_N was much faster in GFP than in GL. Under high PPFDs (>1 180 μmol m^{-2} s^{-1}), significant decreases in q_N were observed in GFP (Fig. 5*B*). Initially, there was a steep increase of ETR values in leaves with increasing PPFD until 450 μmol m^{-2} s^{-1}, after which it formed a plateau and decreased sharply when PPFD reached 880 μmol m^{-2} s^{-1}. Values of ETR in GFP increased initially and peaked around PPFD of 280 μmol m^{-2} s^{-1}. A rapid decrease of ETR was observed after that and it reached zero at PPFD of 2 500 μmol m^{-2} s^{-1} (Fig. 5*C*).

Discussion

We have previously reported that purple colour petals and sepals of CAM *Dendrobium* cv. Sonia flowers were capable of photosynthesis, though their Chl content, PS2 efficiency (F_v/F_m), and carbon fixation rates were lower than those of leaves (Khoo *et al.* 1997, He *et al.* 1998). Non-green petals and sepals of CAM *Dendrobium* cv. Sonia flowers required a lower amount of radiant energy than other green organs of the plant (Khoo *et al.* 1997). We found that under its original shade condition, GFP of cv. Burana Jade exhibited about 50 % of photosynthetic capacities (P_{max} and CAM acidity, Fig. 1) of GL. Photosynthetic capacities were higher in GFP of cv. Burana Jade than in purple colour flower petals of cv. Sonia reported previously (Khoo *et al.* 1997, He *et al.* 1998). Additional photosynthetic sources benefit the developing florescence as many of shade grown orchids are source limited (He *et al.* 2004). In the present study, we found that transferring cv. Burana Jade from shade to intermediate sunlight enhanced P_{max} and CAM acidity compared to plants grown under the shade. This is consistent with our previous conclusion with C_3 orchid *Oncidium* cv. Gower Ramsey that enhanced photosynthetic capacities could be achieved in certain local commercial orchid plants by transferring the shade grown plants to intermediate sunlight (He *et al.* 2004). Unfortunately, leaves of cv. Burana Jade exposed to full sunlight had reduced photosynthetic capacities (Fig. 1). Moreover, increasing growth irradiances did not enhance photosynthetic capacities of GFP. Instead, their photosynthetic capacities were diminished after exposing to intermediate and full sunlight (Fig. 1). Reduced photosynthetic capacities of GFP after transfer to HI were significantly correlated with their higher susceptibility to HI as compared to that of GL. This was reflected from the differences in Chl fluorescence and Chl content between GL and GFP exposed to different growth irradiances to be discussed below.

Predawn and midday F_v/F_m and Chl content obtained from GL grown at different growth irradiances indicate that leaves of cv. Burana Jade could utilise intermediate sunlight under a maximal PPFD of 500–600 µmol m^{-2} s^{-1} although this orchid is normally grown under shade with a maximal PPFD of 200–300 µmol m^{-2} s^{-1} in the local commercial nursery (Figs. 2–4). However, continued decreases in predawn and midday F_v/F_m of full sunlight leaves throughout the 35 d of treatment (Figs. 2*A* and 4*B*) were observed. The lower F_v/F_m values indicate that a decrease in the PS2 efficiency occurred in GL and GFP. Moreover, they were incapable to recover in the night. Decreased P_{max} (Fig. 1) as a result of prevailing full sunlight treatment is a quantifiable consequence of chronic photoinhibition (Osmond 1994). This was earlier observed in *Heliconia* grown under natural tropical conditions (He *et al.* 1996) and in cv. Sonia grown under natural tropical conditions (He *et al.* 1998). As discussed above, reductions of photosynthetic capacities of leaves were observed when plants were transferred from shade to full sunlight. This indicates that full sunlight with a PPFD higher than optimal grown irradiance (about 600 µmol m^{-2} s^{-1}) saturates photosynthesis of these plants. This was reflected by strong reduction of both q_P (Fig. 5*A*) and ETR (Fig. 5*B*) and increase in q_N (Fig. 5*A*). Chl fluorescence provides a feasible *in vivo* determination of photosynthetic radiant energy utilisation, particularly during stomatal closure at light phase of CAM, where application of gas exchange is not readily accessible (Khoo *et al.* 1997). The recorded values of q_P in the laboratory of the present study of around 0.4, when the leaves were irradiated with a PPFD of 880 µmol m^{-2} s^{-1} (Fig. 5*A*), were below the empirical threshold for chronic photoinhibition (Öquist *et al.* 1992). Leaf chronic photoinhibition of cv. Burana Jade grown under full sunlight was due to the accumulation of dynamic photoinhibition (decreased midday F_v/F_m) (Fig. 4*B*) on bright sunny days when midday PPFD was around 1 200 µmol m^{-2} s^{-1} (Fig. 4*A*). When irradiation became saturating for photosynthesis, the allocation of excitation energy determined by q_N increased when q_P decreased with increasing PPFD (Fig. 4*A*) (Demmig and Winter 1988). q_N, associated with thermal dissipation of excitation energy, plays an important role in photoprotection (Chow 1994). The breakdown of Chl is associated with the reduction in photosynthetic capacity induced by excessive photons (Fig. 3; Lichtenthaler *et al.* 1981, He *et al.* 1996).

Photoinhibitory damage occurred in GFP not only in plants exposed to full sunlight but also in those exposed to intermediate sunlight (Figs. 2*B* and 4*C*). This was supported by the field measurements of decreased predawn and midday F_v/F_m (Figs. 2 and 4) and decreased Chl content of GFP in plants exposed to both full sunlight and to intermediate sunlight, over the 35 d (Fig. 3*B*,*C*). The chlorotic symptoms were more severe in GFP than in GL. Under full sunlight, GFP were also photobleached and very low Chl content was detected (Fig. 3*C*). The radiant energy requirement for GFP was much lower than that of GL. For example, compare a rapid drop in q_P and ETR in the GFP as the PPFD increased above 280 µmol m^{-2} s^{-1} and the constant rates of q_P and ETR in GL under PPFD between 280–650 µmol m^{-2} s^{-1} (Fig. 5). Lower radiant energy requirement by non-green floral parts than by GL were reported by the same research team in CAM plant *Dendrobium* (Khoo *et al.* 1997) and in cv. Sonia petals (He *et al.* 1998). The processes of not only the photon energy use in PS2 (q_P and ETR) but also dissipation of excess photon energy (q_N) are important for avoiding photoinhibition under HI. For GFP, the q_N value reached its maximal at much lower PPFDs than that for GL (Fig. 5*A*). Significant decreases in q_N were also observed in GFP when PPFD was higher than 1 180 µmol m^{-2} s^{-1}. Due to a brief (5 min) exposure of GFP to HI in the laboratory, the decrease in q_N was small. However, under full sunlight, the duration of q_N in plants (or GFP) exposed to PPFDs of 1 100–1 200 µmol m^{-2} s^{-1} was at least 3–4 h on sunny days. Lower q_N values under HI imply that GFP are unable to regulate and protect photosynthesis when photon energy absorption exceeds the capacity for energy utilization. Much higher irradiance stress occurred in GFP than in GL under similar irradiances. All these results indicate that the GFP of plants of cv. Burana Jade were more susceptible to photoinhibition when exposed to HI as compared to their GL. Therefore, GL of this cv. were able to receive more photons than GFP on the same plant. But this has not previously been considered in terms of increasing the growth irradiance of leaf as the GFP located above the leaves were more susceptible to HI. We previously reported that flowers require less radiant energy for photosynthesis, some plants which usually grow in the shade, do not necessarily have to be grown in the shade (Khoo *et al.* 1997). When the cv. Burana Jade plants were transferred from so-called "optimal shade" to intermediate sunlight, increases of P_{max} and CAM acidity of leaves were observed. There were no decreases in Chl content and F_v/F_m in leaves exposed to intermediate sunlight. It, therefore, suggests that cv. Burana Jade, a source-limited shade plant, could increase its source capacity by growing under HI. However, for the whole plant it is a conflict between maximizing photon energy utilisation of leaves to increase P_{max} and CAM acidity and minimising photon absorption of GFP to prevent photoinhibition. Hence, if the particular plant is continually grown in the shade, irradiance limitation may cause a lower photosynthetic rate in the leaves, resulting in a slower growth rate (Lüttge *et al.* 1991). One way of enhancing the photosynthetic rate of the leaves in the cv. Burana Jade is to transfer the plant to intermediate irradiation during the vegetative growth stages. The plant is then transferred back to shade when inflorescence is initiated, so as to prevent photodamage in the flowers. This strategy was previously suggested by He *et al.* (1998).

For the first time, our research team also compared the CAM acidity (TA) of both GL and GFP. The differences in CAM acidity among the different growth irradiances were similar to that of P_{max}, *i.e.* exposure of cv. Burana Jade to HI decreased acid accumulation (Fig. 1*B*). CAM plants are dependent on the organic acids that accumulate overnight in the vacuoles as a source of CO_2 during the daylight de-acidification period, when stomata are closed and HI generally prevails. The internal supply of CO_2 derived from organic acid in CAM plants served to mitigate photoinhibition (Adams and Osmond 1988). Is internal supply of CO_2 of cv. Burana Jade GL and GFP important in determining the photon susceptibility of different plant organs to growth irradiance and the utilisation of their energy? This merits future studies.

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