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Source-to-sink relationship between green leaves and green petals of different ages of the CAM orchid *Dendrobium* cv. Burana Jade

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Abstract

Photosynthetic capacities of green leaves (GL) and green flower petals (GFP) of different ages of the CAM plant *Dendrobium* cv. Burana Jade were studied through chlorophyll (Chl) content, Chl fluorescence characteristic F_v/F_m, maximal photosynthetic O_2 evolution rates (P_{max}), and CAM acidities [dawn/dusk fluctuations in titratable acidity (TA)]. All these photosynthetic parameters were higher in GL than in GFP. Among the different ages of GFP, the young GFP had significant higher readings of all photosynthetic parameters than the oldest GFP, indicating that reduced photosynthesis occurred in the senesced GFP. The source-to-sink relationship between GL and GFP was also studied by comparing the diurnal changes in contents of total soluble and insoluble sugars and TA between the fully irradiated (FI) control (with both irradiated GL and GFP) and GL-darkened plants (covering all GL with aluminium foils, leaving only the GFP exposed to radiation). CAM acidities were much lower in GL darkened with aluminium foils compared to those of FI-GL while there were no differences in CAM acidities of their GFP. The contents of total soluble and insoluble sugars and the CAM acidities of GL towards the end of the day were lower in GL-darkened plants compared to that of FI-plants. Hence CAM acidities of GL depended on their saccharide contents. However, diurnal changes of TA in GFP were similar in all GFP regardless of their ages, with or without GL photosynthetic sources. Thus CAM acidities of GFP are independent of GL saccharides. However, lower saccharide content in GFP (especially the oldest GFP) of GL-darkened plants implies that GFP function as sinks and depend on saccharides exported from GL for its development and growth.

Additional key words: CAM acidity; chlorophyll fluorescence induction; photosynthetic O_2 evolution; saccharides.

Introduction

We have previously reported that green flower petals (GFP) of the CAM plant *Dendrobium* cv. Burana Jade were capable of photosynthesis and also used crassulacean acid metabolism (CAM) for photosynthetic carbon fixation process similarly to its green leaves (GL) (He and Teo 2007). CAM is an important photosynthetic carbon fixation process that allows chloroplast containing cells to fix CO_2 initially at night using phospho*enol*-pyruvate carboxylase (PEPC) in the cytosol. This leads to the formation of C_4 organic acids (usually malate), which are stored in the vacuoles (Cushman 2001, Dodd *et al.* 2002). During daylight, the organic acids are subsequently converted back to CO_2, creating an internal CO_2 source that is re-assimilated by ribulose-1,5-bisphosphate carboxylase/oxygenase in the chloroplasts. As the 3-C substrate, phospho*enol*pyruvate (PEP) is produced *via* the glycolytic breakdown of saccharides formed during the previous day; the recovery of saccharide *via* gluconeogenesis imposes a high energetic cost on the pathway. However, this phase is important as it ensures the production of substrate for subsequent nocturnal carboxylation and partitioning for growth (Cushman 2001, Dodd *et al.* 2002). The saccharides that provide substrates for the nocturnal reactions are transported either into chloroplast and stored as starch or transported into vacuole and stored as sucrose (Borland and Taybi 2004).

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Abbreviations: Chl – chlorophyll; DM – dry matter; F_0 – minimal fluorescence yield of a "dark-adapted" sample; 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; FI – fully irradiated; GFP – green flower petal; GL – green leaf; P_{max} – maximal photosynthetic O_2 evolution rate; PEPC – phospho*enol*pyruvate carboxylase; PPFD – photosynthetic photon flux density; TA – titratable acidity.
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In addition, we previously reported that the partitioning of assimilates in many tropical orchids is source-limited since some of them are shade plants and photoinhibition occurs when they are exposed to high growth irradiance (He *et al*. 1998, 2004, He and Teo 2007). In their flowering stage, particularly for those orchids with large inflorescence, the developing GFP may retain a large proportion of their newly fixed carbon for carbon fixation at night and/or for maintaining its growth. High activities of invertase in the young, rapidly expanding leaves encourage the metabolism of sucrose in the early stages of leaf development, when the young leaves function primarily as sinks (Zamski and Schaffer 1996). Similar to the young developing leaves, the developing GFP may also be functioning as sink although they are capable of photosynthesis. In *Dendrobium* cv. Burana Jade orchids, the photosynthetic rate of GFP was only 40 to 50 % that of the GL (He and Teo 2007). Large saccharide energy drain to the GFP may occur due to the large number of GFP. Changes in petal development stages may further lead to changes in carbon partitioning. Hence, questions addressed in this paper are: (*1*) Do GFP produce sufficient saccharides during the day for their carboxylation (the formation of C_4 organic acids) at night and/or for its development? (*2*) Will saccharides that are produced in the source GL be transported to GFP, which will now be a carbon sink? To answer these questions**,** photosynthetic capacities of GL and GFP of different ages of *Dendrobium* cv. Burana Jade were first compared by the measurements of chlorophyll (Chl) content, photosynthetic O_2 evolution (P_{max}), and F_v/F_m. The source-to-sink relationship between GL and GFP was then studied in GL-darkened plants (leaving only the GFP as the sole source) in comparison to plants that were FI-treated (with both irradiated photosynthetic GL and GFP). CAM acidities and the diurnal changes of saccharides and titratable acidity (TA) were studied between FI-control and GL-darkened plants. Therefore, the main objectives of this study were to determine if the GFP of *Dendrobium* cv. Burana Jade plants act as saccharide source or both source and sink, and also to investigate if different floral developing stages affect the source-to-sink relationship between GL and GFP. The finding may be used by the local orchid growers trying to increase the life span of GFP.

Materials and methods

Plants and experimental design: Mature plants of *Dendrobium* cv. Burana Jade (*Dendronium* Madame Uraiwan × *Dendrobium* May Neal), a CAM orchid, were obtained from a commercial nursery. There were 2 to 3 shoots in each pot and each shoot had two inflorescences. Each inflorescence had 8–9 newly opened flowers, *i.e*. about 30 % of flowers were fully opened. These plants were acclimated for one week under intermediate sunlight, with a maximum midday photosynthetic photon flux density (PPFD) of 600–700 μmol m^{-2} s^{-1} and fluctuating ambient temperature of 24–34 °C. They were watered once a day, and fertilized and sprayed with fungicides twice a week. In order to harvest similar ages of flower from different plants, the GFP were tagged immediately after purchasing, with the last fully expanded GFP marked as GFP0. The old mature GFP grown below GFP0 were labelled with a negative sign, starting with GFP–1 for the inflorescence just below GFP0. Additional young GFP that developed were marked with a positive sign, with the next blooming GFP labelled as GFP+1, then GFP+2, and so on. Time was allowed (10–12 d) for the GFP to grow to GFP+10 before being tested. In order to investigate if the GFP of the *Dendrobium* cv. Burana Jade plants acts as carbon source or sink, all GL of one orchid plant were covered with aluminium foil, leaving only the GFP as irradiated. Hence, for these plants GFP were the only photosynthetic sources. For the control plants, none of the GL was wrapped and hence in control plants both GL and GFP produced photosynthates. The 3rd or 4th GL from the top of each plant at different stages of GFP were harvested for different measurements.

Chl content: 0.05 g of each GL and GFP sample was weighed and cut into small pieces. Chl was extracted from these samples using dimethylformamide, and quantified spectrophometrically at wavelengths of 647 and 664 nm (Wellburn 1994).

Measurements of F_v/F_m were made with Chl fluorometer (Plant Efficiency Analyser, PEA, *Hansatech Instruments*, England) between 07:00 and 08:00 h. The intact GL and GFP were pre-darkened with clips for 15 min prior to measurements. Dark-adapted GL and GFP were then placed under the light pipe and irradiated with the pulsed lower intensity-measuring beam to measure F_0, initial Chl fluorescence. F_m, maximum Chl fluorescence, was assessed by 0.8 s of saturated pulse (6 000 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 photosystem 2 (PS2) reaction centres in dark-adapted plant samples was estimated as F_v/F_m.

Measurement of photosynthetic O_2 evolution (P_{max}) **on detached GL and GFP**: The P_{max} of GL and GFP were determined using a leaf disc O_2 electrode (*Hansatech*, King's Lynn, Norfolk, UK), under an irradiance of 1 000 μmol m^{-2} s^{-1} at 25 °C using GL 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).

TA values of GL and GFP were determined at 06:00, 09:00, 12:00, 15:00, and 18:00 h. Five discs (7 mm dia-

meter) 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 bath of boiling water on a hot plate and left for 15 min. After this, 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 dry matter (DM) was obtained. TA was calculated using the formula TA = (0.01×volume)/DM. CAM acidity, which was the dawn/dusk fluctuation of TA, was calculated from the difference between TA at 09:00 and 18:00 h.

Soluble sugars were extracted using the method of Buysse and Merckx (1994). About 0.05 g of dried GL and GFP samples were extracted three times in 5 cm^3 of hot 80 % ethanol (80 °C). The supernatants were pooled and made to a convenient volume. An aliquot (1 cm^3) of 5 % (m/v) phenol was added to 1 cm^3 of the plant extract, followed by 5 cm^3 of concentrated H_2SO_4, and mixed thoroughly. The reaction mixture was allowed to stand for 30 min before the absorbance was recorded at 490 nm using a spectrophotometer. Total sugar content of the sample was calculated using a calibration curve from a glucose working standard.

Insoluble sugars were extracted from the residual plant material from the soluble sugar extraction described above. This was done by incubating the dry pellet with 5 cm^3 of 3 % HCl in a boiling water bath for 3 h. The soluble products were assayed by the same phenol-sulphuric method described above.

Statistical analysis: Data from each experimental treatment was assessed using *t*-test and one-way analysis of variance (ANOVA) on *MINITAB*, release *14.12*, 2004.

Results

Photosynthetic characteristics of GL and GFP: The Chl content, F_v/F_m, P_{max}, and CAM acidities of GL and GFP are shown in Fig. 1*A–D*, respectively. The GL exhibited significantly higher values in all parameters than the GFP (p<0.05). GFP–8, the oldest GFP, displayed significantly lower readings of all parameters than the youngest GFP+8 (p<0.05). However, there were no significant differences in all parameters between GFP+8 and other GFP.

CAM acidities of the FI-control and GL-darkened plants: There was a marked decrease in CAM acidity of GL in GL-darkened plant compared to that of FI-control plant on any of the three consecutive sunny days (Fig. 2; p<0.05). For instance, on the same day (*i.e.* day one) of start of the GL-darkening treatment, CAM acidity of GL decreased by 34 % (Fig. 2*A*), and further decreased by 52 % (Fig. 2*B*) and 63 % (Fig. 2*C*) on days 2 and 3, respectively, compared to that of FI-control plants. Although all GFP had significant lower CAM acidities than GL (p<0.05), there were no significant differences in CAM acidities of GFP between the FI-control and GL-darkened plants on all the three sunny day regardless of their ages. However, among the different ages, CAM acidity of GFP–8 was significant lower than that of all the other younger GFP, which was similar to the results illustrated in Fig. 1*D*.

Saccharides and titratable acidity (TA) of the FI-control and GL-darkened plants: Fig. 3 shows the diurnal changes in total soluble sugars (*A–C*), insoluble sugars (*D–F*), and TA (*G–I*) in GL of the FI-control and GL-darkened plants on three consecutive sunny days. The

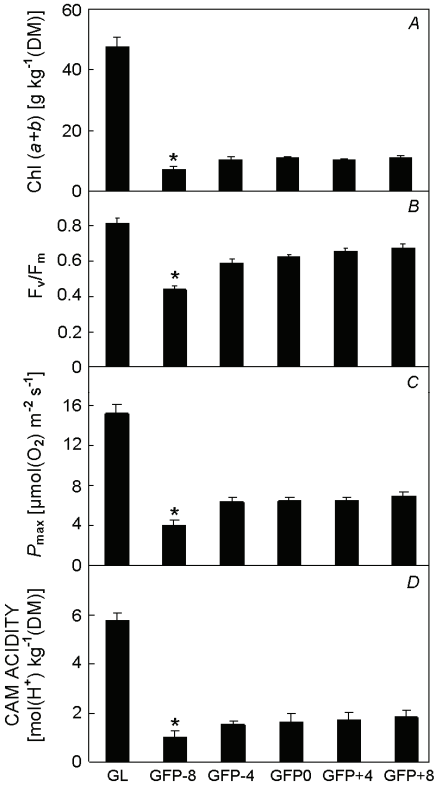

Fig. 1. Chlorophyll (Chl) content (*A*), F_v/F_m (*B*), maximum photosynthetic rate, P_{max} (*C*), and CAM acidities (*D*) of GL and GFP of different ages of *Dendrobium* cv. Burana Jade. Means of four measurements of four different GL and four different GFP. *Vertical bars* represent standard errors. All readings of GL showed significant differences to that of all GFP. *significant difference between other GFP and GFP+8, the youngest GFP.

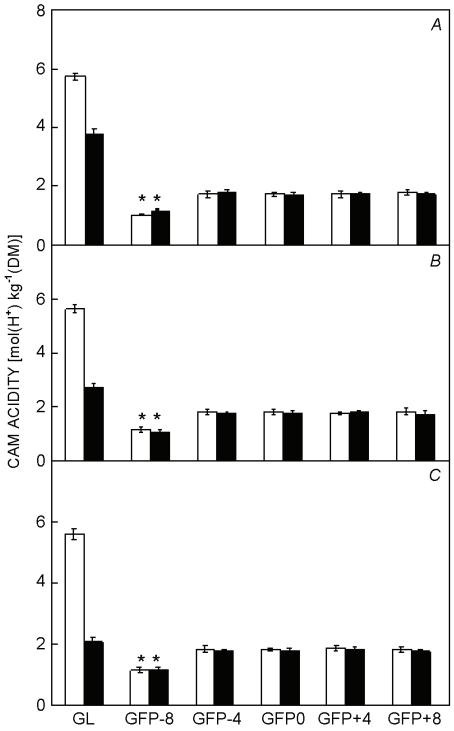

Fig. 2. CAM acidities of GL and GFP of FI-control (□) and GL-darkened (■) *Dendrobium* cv. Burana Jade on three consecutive sunny days (*A, B, C*). Means of four measurements of four different GL and four different GFP. *Vertical bars* represent standard errors. *significant difference between other GFP and GFP+8, the youngest GFP.

GL of FI-control plants exhibited significant increases in both soluble and insoluble sugars during the day (Fig. 3*A–F*), indicating that *Dendrobium* cv. Burana Jade stored both soluble and insoluble sugars in their GL. Darkening of all GL had significant effects on both total soluble and insoluble sugars as compared to that of FI-control plants at any given time of the day. For instance, the total soluble and insoluble sugar contents of GL were much greater in FI-control plants than in GL-darkened plants ($p<0.05$). On day one, *i.e*. the day of starting treatment, however, significant increase of soluble sugars was still obtained in GL by totally darkening them over the course of the day (Fig. 3*A*) while the content of insoluble sugars was drastically decreased in the same GL samples (Fig. 3*D*). These results imply that increases of soluble sugar contents in the darkened-GL may be due to the hydrolysis of insoluble sugars stored in the GL before treatment. On days 2 and 3 of the GL-darkening treatment, the amounts of soluble sugars in GL were consistently lower during the day (Fig. 3*B,C*) and content of insoluble sugars in the same GL samples continually decreased (Fig. 3*E,F*). On day 1 of GL-darkening treatment, TA of GL at any given time from 09:00 h was higher in GL darkened plants than in FI-control plants ($p<0.05$; Fig. 3*G*). At the end of the photoperiod, the dawn-dusk difference in TA, *i.e*. the CAM acidities of GL (the differences of TA between 06:00 and 18:00 h) were 5.75 and 3.98 mol(H^+) kg^{-1}(DM), respectively, for the FI- and GL-darkened plants. On days 2 and 3, the TA of GL was much lower in samples harvested at 06:00 h in GL-darkened plants than in FI-control plants (Fig. 3*H,I*).

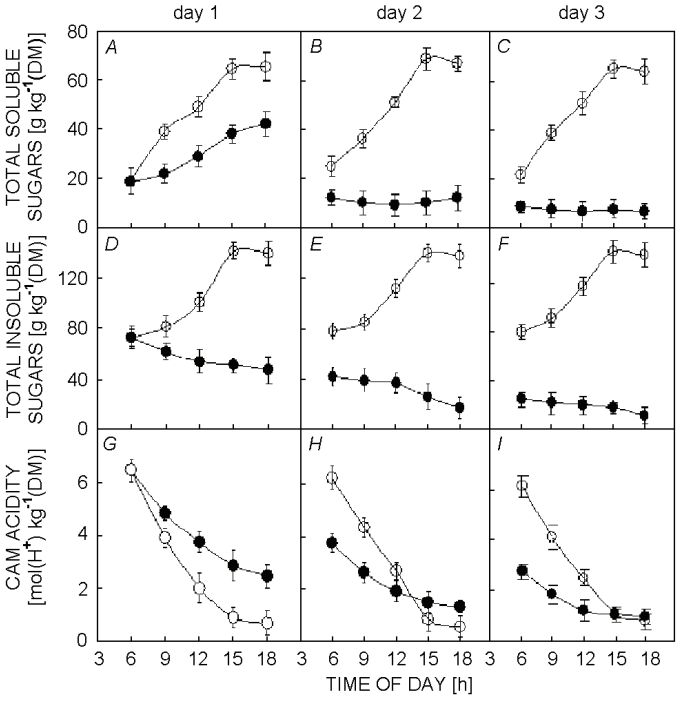

Fig. 3. Diurnal changes of total soluble sugars (*A–C*), insoluble sugars (*D–F*), and titratable activity (*G–I*) in GL of FI-control (○) and GL-darkened (●) *Dendrobium* cv. Burana Jade on three consecutive sunny days. Means of four measurements of four different GL and four different GFP. *Vertical bars* represent standard errors.

Moreover, the GL-darkened plants had much lower decarboxylation rates in their GL as compared to FI-plants. For instance, CAM acidities of GL were 5.31 and 1.77 mol(H^+) kg^{-1}(DM), respectively, for the fully GL-darkened plants and FI-plants on day 3.

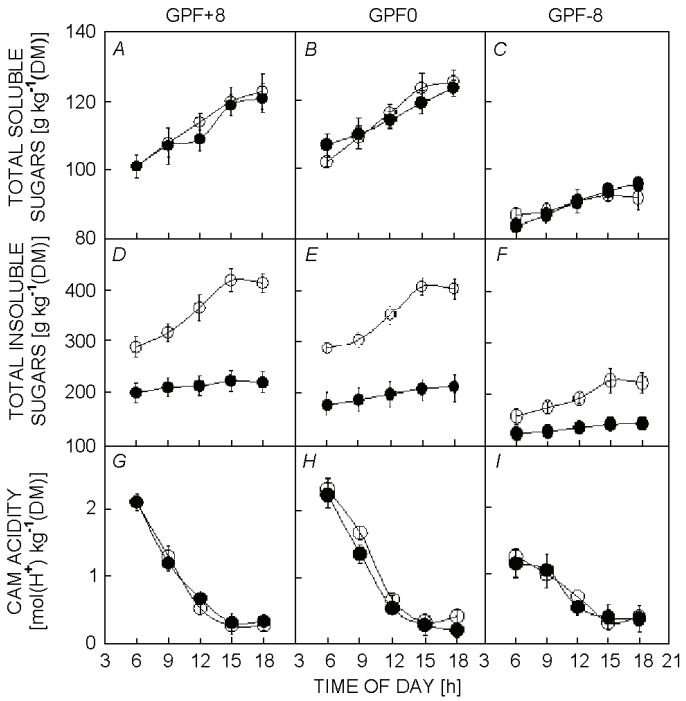

Fig. 4. Diurnal changes of total soluble sugars (*A–C*), insoluble sugars (*D–F*), and titratable activity (*G–I*) in different GFP of FI-control (○) and GL-darkened (●) *Dendrobium* cv. Burana Jade on day 3 (a sunny day) after treatment. Means of four measurements of four different GL and four different GFP. *Vertical bars* represent the standard errors.

The effects of removing GL photosynthetic sources on the contents of total soluble and insoluble sugars and TA of GFP+8, GFP0, and GFP–8 were analysed on days 1, 2, and 3 after all GL were darkened. The results for three consecutive sunny days were similar. Hence, only the data of day 3 are shown in Fig. 4. Increases in soluble sugars during the day were observed in all GFP. For the same position of GFP, there were no significant differences in the total soluble sugars between the FI- and GL-darkened plants (Fig. 4*A–C*). However, the rate of accumulation of total soluble sugars was significant lower in GFP–8 (Fig. 4*C*) than in GFP0 (Fig. 4*B*) and GFP+8 (Fig. 4*A*). The contents of insoluble sugars of all GFP increased markedly in the FI-plants from 06:00 to 15:00 h and then remained constant and high towards the end of the photoperiod. Similar to that of total soluble sugars, GFP-8 had lower increases in total insoluble sugars than GFP0 and GFP+8. However, there were no significant increases in content of total insoluble sugars of all GFP in GL-darkened plants (Fig. 4*D–F*). There were no differences in TA of GFP at any given time during the day between FI-and GL-darkened plants (Fig. 3*G–I*).

Discussion

Khoo *et al*. (1997) found that purple petals of CAM *Dendrobium* cv. Sonia are capable of photosynthesis, though their Chl content, PS2 efficiency (F_v/F_m), and carbon fixation rates were lower than those of leaves. He and Teo (2007) also reported that the photosynthetic rate of GFP of *Dendrobium* cv. Burana Jade was only 40–50 % that of GL. Our present results confirmed that photosynthetic rates of orchid GFP were much lower than those of GL (Fig. 1). For all GFP tested (from GFP+8 to GFP–7 position), with the exception of GFP–8, there were no significant differences in photosynthetic parameters among other GFP. Similar results were observed in the study of Chl content in *Dendrobium* cv. Sonai flowers of different developmental stages (Khoo *et al.* 1997).

Photosynthetic sources are organs or tissues that produce more assimilate than they require for own metabolism and growth. Thus, they are net exporters or producers of photoassimilates (Zamski and Schaffer 1996). GFP of tropical orchids function as additional photosynthetic organs which may be due to the fact that many tropical orchids are shade plants and they are source-limited (He *et al*. 1998, 2004). Similar to the developing leaves (Zamski and Schaffer 1996), young developing GFP of CAM orchids may retain a large proportion of their newly fixed carbon for carbon fixation at night and/or for maintaining their growth. Hence, they can function primarily as sinks. As photosynthetic capacities of GFP were much lower than those of GL (Fig. 1), the main question is whether the newly fixed

carbon by GFP is adequate for its carbon fixation at night and/or for maintaining its growth and development. As the *Dendrobium* cv. Burana Jade has both GL and GFP functioning as photosynthetic organs, in order to investigate the physiological roles of GFP we darkened all GL to remove their source capacity. In comparison to the FI-plants, CAM acidities of GFP were not affected by removing the source capacities of GL (Fig. 2). These data indicate that newly fixed carbon by GL and photosynthesis of GFP had no direct relationship. Although all GL were enclosed with aluminium foil and kept in total darkness, de-acidification (*i.e*. decease in TA) still occurred during the day. However, CAM acidities (the rate of de-acidification) of GL-darkened plants decreased drastically from the start of treatment and they decreased in following days (Fig. 2). This was further confirmed by the results of another experiment (Fig. 3*G–I*). Furthermore, Fig. 3 shows that not only TA (thus CAM acidities) but also contents of soluble and insoluble sugars of GL were affected immediately by darkening of GL. Decreases in TA and CAM acidities of GL during the first day of covering GL with aluminium foil could be due to the lack of newly produced chemical energy such as ATP and NADPH generated by light reactions and required for CO_2 reduction by Calvin cycle. Furthermore, the energy requirement for carbon flow of the CAM cycle is higher than in C_3 photosynthesis (Winter and Smith 1996). During the decarboxylation (Phase III of CAM photosynthesis), gluconeogenic recovery of storage saccharides imposes a high energetic cost on the pathway, which is suported by increased rates of photosynthetic electron transport during this stage (Maxwell *et al*. 1999, de Mattos and Lüttge 2001) and the rate of decarboxylation is strictly light-dependent (Dodd *et al*. 2002). In the present study, when all GL were darkened, the rate of decarboxylation decreased immediately (Fig. 3). Further deceases in TA and CAM acidities on days 2 and 3 of GL-darkened treatment could result from both lack of newly produced chemical energy and lower saccharide content stored in the darkened GL. Previous irradiance determines the degree of nocturnal organic acid accumulation during the subsequent dark period as light-driven photosynthesis and gluconeogenesis furnish the saccharide stores required for PEP synthesis *via* glycolysis during the dark period as a precursor for phase I CO_2 fixation by PEPC (Nobel and Hartsock 1983). Our results also show that *Dendrobium* cv. Burana Jade stored both soluble and insoluble sugars in their GL and GFP during the photoperiod. Both GL and GFP stored much more insoluble sugars than soluble sugars (Figs. 3 and 4). Insoluble sugars (starch and glucans) stored in the chloroplasts may account for the required conservation of carbon (Christopher *et al*. 1996). For GFP, although the content of soluble sugars was much larger than that of GL of FI-plants, the amount of soluble sugars accumulated during the day was much lower in GFP (Fig. 4*A–C*) than in GL (Fig. 3*A–C*), which could be partly due to their lower photosynthetic capacities compared to those of GL (Fig. 1). However, unlike soluble sugars, the GFP of FI-plants accumulate much more insoluble sugars during the day. For active and developing GFP, they stored more than twice the amount of insoluble sugars than GL over a 12-h of photoperiod. Furthermore, compared to that of GFP of GL-darkened plants (Fig. 4*D–F*), the accumulation of insoluble sugars was much higher in GFP of FI-plants. Based on these results, despite the lack of direct measurement of export photoassimilate from GL to GFP, it is clear that darkening of GL drastically reduced the amount of insoluble sugars of GFP which were exported from GL. In their review article on the mechanisms that synchronize the supply and demand for carbon whilst maintaining photosynthetic plasticity over the 24-h CAM cycle, Borland and Taybi (2004) concluded that there are reciprocate fluctuations in malate and saccharide contents which may represent up to 20 % of leaf DM. In the present study, saccharide contents (sum of total soluble and insoluble sugars) for GL were about 10 % and more than 20 % of their DM, respectively, at the beginning and by the end of the photoperiod (Fig. 3) in the FI-plants. For the young GFP of FI-plants, the saccharide contents at the beginning and by the end of the photoperiod, respectively, represented up to 40 % and more than 50 % of their DM (Fig. 4). However, the content of insoluble sugars in GFP of GL-darkened plants remained much lower than that in FI-plants. Due to their lower accumulation of insoluble sugars, the GFP of GL-darkened plants had significantly lower DM than the FI-control plants (data not shown). Thus GFP act as a very strong saccharide sink and can transport large amount of saccharides from GL. For senescent GFP–8, the saccharide content was much lower, less than 20 % of its DM at dawn and there was much slower increase over the whole photoperiod compared to young GFP. In the study with daylily (*Hemerocallis* cv. Cradle Song) flower, Bieleski (1995) reported that over a 12-h period the expanding flower switched from acting as a strong saccharide sink to a strong source during senescence. During senescence, petals of attached daylily flowers lost 95 % of sugars and 65 % of DM over the first 24 h, with 30 % of DM loss coming from non-sugar components. Our study also showed that the DM of GFP–8 was about 50 % of other young GFP (data not shown). Similar changes in TA of GFP in both FI- and GL-darkened plants over the course of the day (Fig. 4*G–I*) further supported that *Dendrobium* cv. Burana Jade, which stored insoluble sugar in both GL and GFP, could account for the required conservation of carbon (Christopher and Holtum 1996). On day 3 of GL-darkening, the content of insoluble sugars in GFP of GL-darkened plants was about 100 g kg^{-1}(DM) (Fig. 4*D–F*), which was similar to that of GL of FI-plants (Fig. 3*D–F*). These results imply that the higher conservation of insoluble sugars in GFP before darkening their GL may partially account for the C required in the dark for the formation of the C_4 malic acid. This could explain

why there were no differences in TA and CAM acidities of all ages of GFP between FI- and GL-darkened plants. High insoluble sugars accumulating in all GFP also indicate that they are strong sinks. Studying 11 CAM species, Christopher and Holtum (1996) postulated that variation in saccharide partitioning among CAM species resulted from: (*a*) constraints imposed by the CAM syndrome itself, and (*b*) diversity in biochemistry resulting from different evolutionary histories. Patterns of carbon allocation and partitioning between GL and GFP of *Dendrobium* cv. Burana Jade have yet to be investigated. Since the amount of total sugars (soluble and insoluble) in all GFP decreased in GL-darkened plants, all ages of GFP relied on the saccharides from the GL sources for its development and maintenance. Thus, all GFP primarily function as carbon sinks even though they can photosynthesise. With sugar starvation, the GFP may undergo a faster rate of senescence. This was supported by the fact that there were considerably lower photosynthetic capacities (Fig. 1) and sugar contents (Fig. 4) in the senesced GFP-8. Meanwhile, juvenile GFP had greater sugar contents, which was the result of higher photosynthetic capacities. Hence there was a substantial interaction between development stage of GFP and photoassimilates exported from the source GL. Doorn (2004) reported that *Arabidopsis* leaves kept in darkness induced the expression of senescence-associated genes resulting from low saccharide contents. Effect of saccharide contents on the senescence of orchid GFP, therefore, merits our future research. In our previous study with *Dendrobium* cv. Burana Jade we suggested an increase in photosynthetic rate of GL prior to initiation of inflorescence by growing them under high irradiance and then transferred the plants back to shade to prevent photodamage in GFP (He *et al*. 2007). Based on the results of the present study, understanding the pattern of carbon partitioning between GL and GFP of *Dendrobium* cv. Burana Jade would be another important step toward understanding the basis for the growth and development and the life span of GFP.

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