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Photosynthetic utilization of radiant energy by CAM *Dendrobium* flowers

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Abstract

$^{14}CO_2$ fixation was observed in orchid *Dendrobium* flowers, its rate decreased with the flower development. Chlorophyll (Chl) fluorescence in different developmental stages of flowers was compared to other green plant parts (leaf, inflorescence stalk, and fruit capsule). The photochemical efficiency of photosystem 2 (PS2) (F_v/F_m) of a leaf was 14-21 % higher than that of a mature flower perianth (sepal, petal, and labellum) which had a much lower total Chl content and Chl *a*/*b* ratio. A higher quantum yield of PS2 (Φ_{PS2}) than in the mature flowers was observed in all green parts. Flower sepals had higher Chl content, Chl *a*/*b* ratio, and F_v/F_m values than the petal and labellum. During flower development the Chl content, Chl *a*/*b* ratio, F_v/F_m, and q_N decreased while Φ_{PS2} and q_P remained constant. An exposure of developing flowers to irradiances above 50 μmol m^{-2} s^{-1} resulted in a very drastic drop of Φ_{PS2} and q_P, and a coherent increase of q_N as compared to other green plant organs. A low saturation irradiance (PFD of 100 μmol m^{-2} s^{-1}) and the increase in q_N in the flower indicate that irradiation stress may occur since there is no further protection when the flower is exposed to irradiances above 100 μmol m^{-2} s^{-1}. A low Chl/carotenoid ratio in mature flower perianth as a consequence of Chl content reduction in the course of flower development suggests a relief of irradiation stress *via* this mean.

Additional key words: carotenoids; $^{14}CO_2$ fixation; chlorophyll fluorescence; irradiation stress; saturation irradiance.

Introduction

One way of improving harvestable yield of orchid is to increase the photosynthates pool in source leaves and other Chl-containing organs including the harvestable sink. This can be achieved by an optimizing photosynthetic utilization of radiant energy

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via different plant organs. Carbon fixation of orchid leaves and some non-foliar organs *e.g.* root, pseudobulb, and fruit capsule were studied (Arditti 1992). Even the green *Cymbidium* orchid flower photosynthesizes (Denker and Arditti 1968), its $^{14}CO_2$ fixation rate is about 10 % of the leaf. $^{14}CO_2$ fixation was reported also in *Dendrobium* (Goh 1983) and *Oncidium* orchid flowers (Yong and Hew 1995) whose pigment compositions differ from those of the leaves. Photochemical efficiency of PS2 in *Petunia* corolla is lower than in green leaves (Weiss *et al.* 1988). The capacity of flowers to photosynthesize (Bazzaz and Carlson 1979, Bazzaz *et al.* 1979, Vu *et al.* 1985, Vemmos and Goldwin 1993, 1994) varies, and the variations in their photosynthetic performance at different developmental stages are reflected by fluctuation in dry matter accumulation, Chl content, and CO_2 gaseous exchange pattern (Werk and Ehleringer 1983, Heilmeier and Whale 1987). If the capacity of photosynthetic radiant energy utilization and the dissipation of excited energy in brightly coloured orchid flowers differ from those of leaves, or at various developmental stages, is not known. This paper reports photosynthesis and the photosynthetic utilization of radiant energy in a tropical orchid flower at three developmental stages.

Materials and methods

Plants: Mature *Dendrobium* plants cv. Sonia (*D.* Gracia Lewis × *D.* Lady Constance), a sympodial CAM orchid, were obtained from a commercial orchid nursery. The plants were acclimatized for one week in a greenhouse under an average irradiance of 200 μmol m^{-2} s^{-1} and 32 °C temperature at noon. They were fed twice a week with 1.6 kg m^{-3} of foliar fertilizer (*67, Blue Sky Agricultural Supplies*, Singapore; N:P:K of 13.5:27:27). Plants with one inflorescence and two backshoots were selected. Tight bud, TB (flower No. 3), juvenile open flower, JO (flower No. 4), and mature flower, MF (flower No. 7) along a 50 % blooming stage inflorescence (7-9 flowers) were arbitrarily labelled based on dry mass (values not shown). Fruit capsules were induced by pollinating *Dendrobium* Sonia flowers with *Dendrobium* Bangkok White. Leaf 2 from the apex of current shoot was used.

$^{14}CO_2$ fixation: Plant samples were harvested at 13:00 h, and acclimated in a $^{14}CO_2$ feeding chamber for 15 min under 50 μmol(photon) m^{-2} s^{-1}. $^{14}CO_2$ (1.91 MBq mol^{-1}, *Amershan International*, U.K.) was generated in a small assimilation vial within the chamber using an excess of 0.1 M H_2SO_4 for a single 10 mm^3 droplet of $Na_2{}^{14}CO_3$ (19 MBq). Uptake of $^{14}CO_2$ was allowed for 1 h and followed by immediate immersion of the plant samples into liquid nitrogen. The samples were dried for a week in an 80 °C oven, then the fixed $^{14}CO_2$ was determined by flame oxidation (*Packard Sample Oxidizer* model *307*). The $^{14}CO_2$ released was trapped in *carbosorb E* (*Packard*). Scintillation cocktail (*Permafluor E+*, *Packard*) was added to the liquid sample for radioactivity count by a *Beckman LS6000I* scintillation counter.

Chl and carotenoids (Cars) were extracted by N,N-dimethylformide (DMF) as described by Wellburn (1994). Chl *a*, Chl *b* and Cars absorbances were measured at 647, 664, and 480 nm, respectively, using a *Shimadzu* spectrophotometer *UV-160-02*.

Chl fluorescence was determined using a modulated fluorescence system (*PAM-2000*, *Walz*, Effeltrich, Germany) at 25 °C. The measuring beam [655 nm, 0.1 μmol (quantum) m^{-2} s^{-1}, modulated at 20 kHz], saturating pulse [3000 μmol(quantum) m^{-2} s^{-1}, $\lambda < 710$ nm], modulated actinic red ($\lambda_{max} = 655$ nm) and far-red ($\lambda_{max} = 735$ nm) were delivered to various plant parts separately *via* a fiber optic supported by a leaf clip holder at an angle of 60°. On-line measurements of photochemical efficiency of PS2 (F_v/F_m), photochemical quantum yield (Φ_{PS2}), photochemical quenching (q_P), and non-photochemical quenching (q_N) were taken. Samples for Chl fluorescence determination were freshly harvested at 10:00 h. F_v/F_m was measured after 15 min dark adaptation, followed by sequential exposure of specific red actinic radiation (50 μmol m^{-2} s^{-1}), saturated radiation pulse and far-red radiation for other on-line determinations. Calculations of Φ_{PS2}, q_P, and q_N followed after Genty *et al.* (1989). Irradiance response of Chl fluorescence was determined similarly to Haldimann *et al.* (1996). After the initial F_v/F_m determination, the sample was exposed to specific actinic radiation source (25, 50, 100, 150 μmol m^{-2} s^{-1}) until steady state was reached before five saturated radiation pulses were given to determine Φ_{PS2}, q_P, and q_N. Intervals between pulses were 1 min accompanied by a far-red radiation.

Results

$^{14}CO_2$ fixation by flowers parts at different developmental stages of growth: The highest fixation rate was observed in sepals of flowers, it decreased with flower development in all flower parts (Fig. 1).

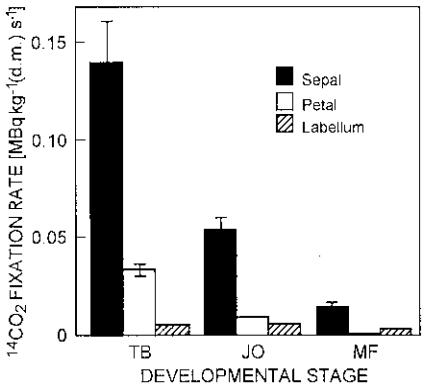

Fig. 1. $^{14}CO_2$ fixation rate of flower at different developmental stages of growth (TB, tight bud; JO, juvenile open flower; MF, mature flower). Each value is the mean ± SE ($n = 7$).

Chl and Car contents in green plant organs and flowers at different developmental stages of flowering: Chl ($a + b$) content and Chl a/b ratio in green *Dendrobium* plant parts (leaf, inflorescence stalk, and fruit capsule) (Fig. 2*A*, *C*) were generally higher than in developing flowers (Fig. 2*B*, *D*). These values in all three different floral

organs were highest during bud stage, but decreased as flower development proceeded. At all flower developmental stages, the sepal had the highest Chl content and Chl *a*/*b*. Also the Car contents in leaf were highest among all plant organs studied (Fig. 2*E*, *F*), they were low in the flower and decreased during flower development (Fig. 2*F*). Chl/Car or $(a + b)/(x + c)$ values in leaf, inflorescence stalk, and fruit capsule were similar but much higher than in flowers (Fig. 2*G*, *H*).

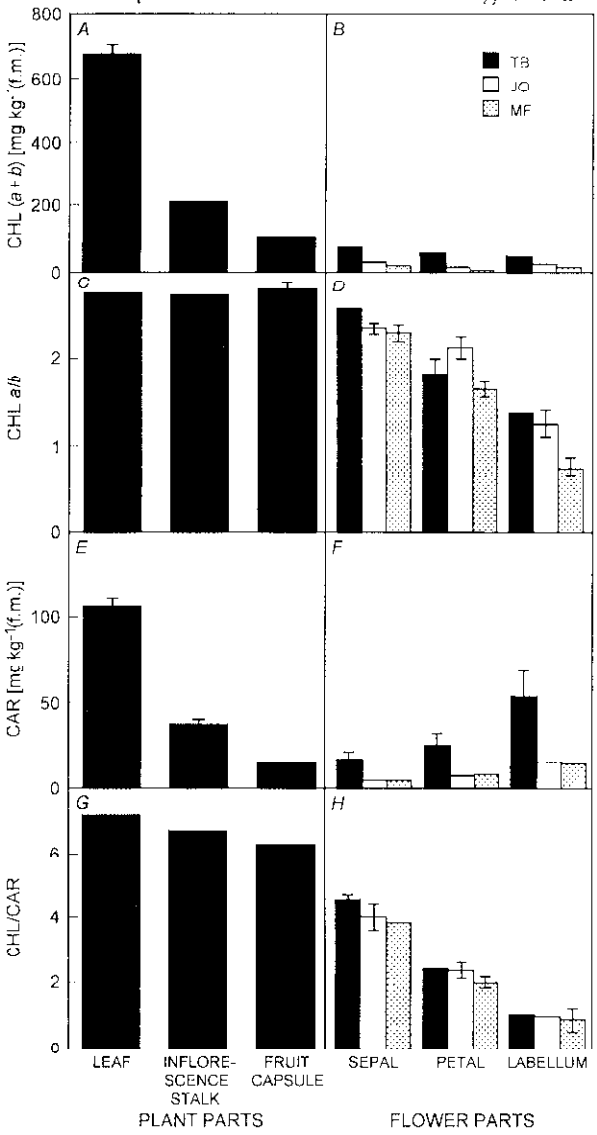

Fig. 2. Chlorophyll (Chl) and carotenoid contents in different plant parts and flower parts of *Dendrobium*. Each value is the mean ± SE ($n = 4$).

Chl fluorescence characteristics in green plant organs and flowers: Preliminary results showed that artifacts in Chl fluorescence determination due to scattering of the

measuring beam caused by a low absorbance of a low content in flowers were not present. This was investigated by measuring background F_0 of a piece of plain white paper. The *PAM-2000* did not produce a significant F_0 of the paper as compared to that of flower (results not shown). The highest photochemical efficiency of PS2 as indicated by F_v/F_m value was found in the leaf (0.83). The F_v/F_m values of the leaf, inflorescence stalk, and fruit capsule were similar (Table 1). The F_v/F_m values of mature flowers were 79-86 % of those of the leaf. In the light, Φ_{PS2} was higher in all green plant parts, q_P was similar in all plant parts but q_N in all flowers was 3 times higher than in the green plant parts.

Table 1. Chlorophyll fluorescence characteristics (photochemical efficiency, F_v/F_m; quantum yield of photosystem 2, Φ_{PS2}; photochemical quenching, q_P, and non-photochemical quenching, q_N) in different plant parts (leaf, inflorescence stalk, fruit capsule and mature flower). F_v/F_m was determined after samples were dark-adapted for 15 min. Φ_{PS2}, q_P, and q_N were determined after reaching steady state in red actinic radiation adaptation at 50 μmol m^{-2} s^{-1}. Each value is the mean ± SE (n = 10 for F_v/F_m, and n = 4 for Φ_{PS2}, q_P, and q_N). Any two means having a common letter are not significantly different at p = 0.05 using DMRT.

Plant parts	Chlorophyll fluorescence characteristics			
	F_v/F_m	Φ_{PS2}	q_P	q_N
Leaf	0.83 ± 0.00^{a}	0.65 ± 0.00^{b}	0.84 ± 0.01^{abc}	0.21 ± 0.04^{bcd}
Inflorescence stalk	0.79 ± 0.01^{a}	0.70 ± 0.02^{a}	0.90 ± 0.02^{ab}	0.11 ± 0.03^{d}
Fruit capsule	0.79 ± 0.00^{b}	0.73 ± 0.01^{a}	0.93 ± 0.01^{a}	0.15 ± 0.05^{cd}
Flower sepal	0.71 ± 0.01^{c}	0.49 ± 0.01^{c}	0.82 ± 0.00^{bc}	0.50 ± 0.06^{a}
Flower petal	0.66 ± 0.01^{d}	0.49 ± 0.02^{c}	0.77 ± 0.04^{c}	0.31 ± 0.08^{bc}
Flower labellum	0.65 ± 0.02^{d}	0.44 ± 0.03^{c}	0.75 ± 0.05^{c}	0.36 ± 0.02^{ab}

Generally, the sepal had the highest F_v/F_m values at all developmental stages of growth (TB, JO, and MF) (Table 2). The F_v/F_m of the flower parts (sepal, petal, and labellum) was decreasing with the development of flowers (Table 2). In the light, a much higher q_N was observed in tight bud, whereas q_P and Φ_{PS2} remained constant during flower development.

Irradiance effects on Chl fluorescence in green plant organs and flowers were examined in leaf, inflorescence stalk, and flower sepals of three developmental stages (TB, JO, MF) (Fig. 3) A decrease in Φ_{PS2} and q_P of all plant parts was observed when the irradiance increased (Fig. 3*A*, *B*). Yet the rates of decrease in flower at all developmental stages were greater than those of the leaf and inflorescence stalk. The Φ_{PS2} of developing flower sepals at 150 μmol m^{-2} s^{-1} was much lower (34 %) than those of the leaves and inflorescence stalk. At irradiances above 50 μmol m^{-2} s^{-1}, q_P in the leaves and inflorescence stalk dropped slightly, but stayed at *ca.* 0.8-0.9. The q_P in developing flowers decreased to as low as 0.4 (Fig. 3*B*). A general q_N increase was observed in all the plant parts studied in response to an increase in irradiance (Fig. 3*C*). The increase in q_N in developing flowers was much higher than that of the

leaf and inflorescence stalk. At 100 μmol m^{-2} s^{-1}, q_N in flower sepals reached saturation at 0.9 while q_N in the leaf and inflorescence stalk was only 0.3.

Table 2. Changes in chlorophyll (Chl) fluorescence characteristics (F_v/F_m, Φ_{PS2}, q_P, and q_N) of three different floral organ parts (sepal, petal, labellum) of *Dendrobium* flower at three developmental stages (TB, tight bud; JO, juvenile open flower; MF, mature flower). F_v/F_m was determined after the samples were dark-adapted for 15 min. Φ_{PS2}, q_P, and q_N were determined after reaching steady state in red actinic radiation adaptation at 50 μmol m^{-2} s^{-1}. Each is the mean ± SE (n = 10 for F_v/F_m, and n = 4 for Φ_{PS2}, q_P, and q_N. Upper case letters represent comparisons among three different floral organs. Lower case letters represent comparisons among three different developmental stages. Any two means having a common letter are not significantly different at p = 0.05 using DMRT.

Chl fluorescence characteristics	Developmental stages TB	JO	MF
F_v/F_m			
Sepal	0.76 ± 0.01^{Aa}	0.70 ± 0.01^{Ab}	0.71 ± 0.01^{Ab}
Petal	0.74 ± 0.01^{Ba}	0.67 ± 0.01^{ABb}	0.66 ± 0.01^{Bb}
Labellum	0.73 ± 0.01^{Ba}	0.65 ± 0.01^{Bb}	0.65 ± 0.02^{Bb}
Φ_{PS2}			
Sepal	0.48 ± 0.02^{Aa}	0.48 ± 0.01^{Aa}	0.50 ± 0.01^{Aa}
Petal	0.44 ± 0.02^{ABa}	0.44 ± 0.00^{Ba}	0.49 ± 0.02^{Aa}
Labellum	0.41 ± 0.02^{Ba}	0.44 ± 0.01^{Ba}	0.44 ± 0.03^{Aa}
q_P			
Sepal	0.83 ± 0.00^{Aa}	0.82 ± 0.00^{Aa}	0.81 ± 0.01^{Aa}
Petal	0.81 ± 0.02^{ABa}	0.83 ± 0.01^{Aa}	0.77 ± 0.04^{Aa}
Labellum	0.78 ± 0.01^{Ba}	0.83 ± 0.01^{Aa}	0.75 ± 0.05^{Aa}
q_N			
Sepal	0.69 ± 0.03^{Aa}	0.55 ± 0.06^{Aab}	0.50 ± 0.06^{Ab}
Petal	0.71 ± 0.03^{Aa}	0.56 ± 0.04^{Aa}	0.30 ± 0.08^{Bb}
Labellum	0.70 ± 0.01^{Aa}	0.58 ± 0.02^{Ab}	0.36 ± 0.02^{ABc}

Discussion

We demonstrated photosynthesis in CAM *Dendrobium* flowers at different developmental stages (Fig. 1). In *Dendrobium*, the sepal was the major flower part responsible for photosynthesis at all stages in terms of a high $^{14}CO_2$ fixation rate (Fig. 1). High values of Chl content and PS2 F_v/F_m in the sepal further supported this observation (Fig. 2*B*, Table 1). On a Chl basis, green parts of reproductive structures such as bracts and calyx have a higher photosynthetic assimilatory capacity than the leaves from the same plant species (Luthra *et al.* 1983, Werk and Ehleringer 1983, Williams *et al.* 1985, Heilmeier and Whale 1987). This may be a developmental advantage because sepals are formed as the outermost whorl covering the reproductive parts particularly during the bud stage. This would maximize radiant energy use efficiency which may result in a higher carbon fixation. In this way, photoassimilates needed for the growth of orchid inflorescence can be supplemented by photosynthesis of flowers *per se*.

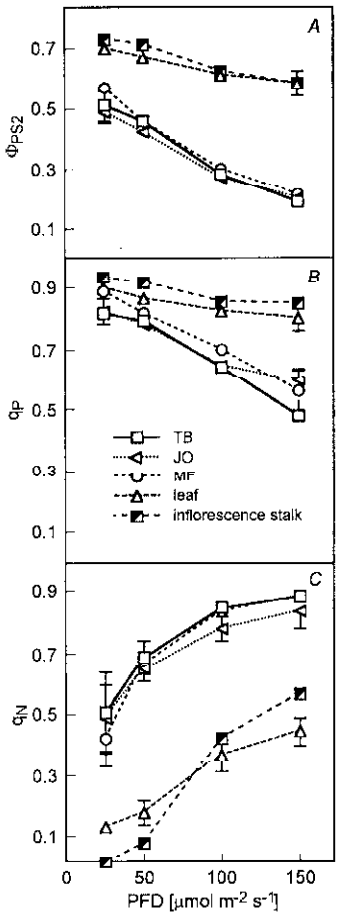

Fig. 3. Irradiance (PFD) effect on quantum yield (Φ_{PS2}), photochemical quenching (q_P), and non-photochemical quenching (q_N) of *Dendrobium* leaf, inflorescence stalk, and flower sepal of three different developmental stages (TB, tight bud; JO, juvenile open flower; MF, mature flower). Samples were supplied with various red actinic irradiances (25, 50, 100, 150 μmol m^{-2} s^{-1}). Each value is the mean ± SE (n = 5).

Chl fluorescence provides a better *in vivo* determination of photosynthetic radiant energy utilization particularly during stomatal closure at light phase of CAM, where application of gas exchange is not readily accessible. In *Dendrobium*, the Chl fluorescence parameters F_v/F_m, Φ_{PS2}, q_P, and q_N differed in various plant parts. Photochemical efficiency of flowers was 14-21 % lower than that of the green plant parts. In *Petunia* corolla, quantum yield of PS2 was 20 % lower than in the leaf (Weiss *et al.* 1988).

Photosynthetic radiant energy utilization of flowers was decreasing with flower age. A lower F_v/F_m possibly relates to a lower photosynthesis in mature *Dendrobium* flower (Table 1). This may also be associated with a decrease in Chl content. It may be argued that a lower Chl content in orchid flowers may result in a high intensity scattered measuring beam from the *PAM-2000* (that is artifacts of higher F_o) and thus a relatively lower F_v/F_m. We found that the F_o signals were almost zero when the target was a piece of white paper. Therefore, lower F_v/F_m values in orchid flower were not an artifact of higher F_o. In *Dendrobium*, the decrease in Chl content during flower development may be a result of chloroplast deterioration to chromoplast at

later stages of flower development as in many anthocyanins-containing flowers (Halevy and Mayak 1981, Brett and Sommekard 1988).

Energy dissipation is reflected by q_N (Schreiber *et al.* 1986). In the *Dendrobium* mature flowers we observed a low q_N, Chl content, and F_v/F_m. This would lead to a decreasing amount of radiant energy harvested by the flower, and thus little energy might be dissipated when the absorbed energy was fully utilized. This may explain the lower q_N found in mature flowers. However, in the tight bud, a high Chl content and a high amount of captured radiant energy may result in an excessive energy for photosynthesis which has to be safely dissipated *via* q_N, hence a higher value.

At limiting PFD, the energy must be captured and utilized efficiently. Excessive PFD must be avoided to prevent photoinhibition. In this study, exposure of orchid flower to a moderate irradiance of 150 μmol m^{-2} s^{-1}, however, caused a more drastic decrease in Φ_{PS2} and q_P as compared to those of the green plant parts. This indicated that *Dendrobium* flower was not as efficient as green plant parts (leaf and inflorescence stalk) in radiant energy utilizing, and the low energy captured may be more than sufficient for photosynthesis of flowers. In the field, *Dendrobium* grows in the shade with a short period of maximum exposure to 500 μmol m^{-2} s^{-1} at noon. A coherent increase in q_N in flowers at 100 μmol m^{-2} s^{-1} may suggest a possible dynamic photoinhibition. A saturation of q_N at 0.9 in flowers as compared to 0.3 in green plant parts indicated that flowers may be unable to protect themselves against radiant stress above 100 μmol m^{-2} s^{-1}. A long-term exposure of orchid flower to a higher PFD may result in chronic photoinhibition. However, *Dendrobium* flowers grown under a low irradiance may have an effective energy dissipation system based upon the Chl/Car ratio. The capacity of xanthophyll cycle in photoprotection against high irradiances was higher in *aurea* tobacco leaves, which had a lower Chl/Car ratio, than in green tobacco leaves (Schindler *et al.* 1994). The carotenoids, particularly those involved in xanthophyll cycle, may play a role in absorption and dissipation of photosynthetic radiation (Björkman and Demmig-Adams 1994, Demmig-Adams and Adams 1996). Of course, the mechanism of photoprotection by zeaxanthin is still open to discussion (Schindler and Lichtenthaler 1994). Nevertheless, in the *Dendrobium* flower parts, the decrease in Chl/Car ratio was due to a reduction in the Chl content during flower development indicating senescence (Fig. 2). Photoinhibition in mature flowers may be minimized by their low Chl contents leading to a lesser amount of excess absorbed radiation. In leaves and roots of *Sarcochilus olivaceus*, the excess absorbed radiation dictates the size of xanthophyll pool and not the incident PFD (Logan *et al.* 1996). Further work is also needed to understand the protective mechanism of flower against radiant stress by a reduction in Chl content during flower development.

In practice, care must be taken in the optimization of irradiance for photosynthesis of orchid plants. This is attributed to the findings that the radiant energy requirement for photosynthesis of flowers is lower than that of other green plant organs, and irradiances above 100 μmol m^{-2} s^{-1} may cause photoinhibition in flowers but not in the leaf.

References

Arditti, J.: Fundamentals of Orchid Biology. - J. Wiley and Sons, New York 1992.

Björkman, O., Demmig-Adams, B.: Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. - In: Schulze, E.-D., Caldwell, M.M. (ed.): Ecophysiology of Photosynthesis. Pp. 17-47. Springer-Verlag, Berlin - Heidelberg 1994.

Bazzaz, F.A., Carlson, R.W.: Photosynthetic contribution of flowers and seeds to reproductive effort of an annual colonizer. - New Phytol. **82**: 223-232, 1979.

Bazzaz, F.A., Carlson, R.W., Harper, J.L.: Contribution to reproductive effort by photosynthesis of flowers and fruits. - Nature **279**: 554-555, 1979.

Brett, D.W., Sommekard, A.P.: Ultrastructural development of plastids in the epidermis and starch layers of glossy *Ranunculus* petals. - Ann. Bot. **58**: 903-910, 1988.

Demmig-Adams, B., Adams, W.W., III: The role of xanthophyll cycle carotenoids in the protection of photosynthesis. - Trends Plant Sci. **1**: 21-26, 1996.

Deuker, J., Arditti, J.: Photosynthetic $^{14}CO_2$ fixation by green *Cymbidium* (*Orchidaceae*) flowers. - Plant Physiol. **43**: 130-132, 1968.

Genty, B., Briantais, J.-M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. - Biochim. biophys. Acta **990**: 87-92, 1989.

Goh, C.J.: Rhytms of acidity and CO_2 production in orchid flowers. - New Phytol. **93**: 25-32, 1983.

Haldimann, P., Fracheboud, Y., Stamp, P.: Photosynthetic performance and resistance to photoinhibition of *Zea mays* leaves grown at sub-optimal temperature. - Plant Cell Environ. **19**: 85-92, 1996.

Halevy, H.A., Mayak, S.: Senescence and postharvest physiology of cut flowers. Part 2. - Hort. Rev. **3**: 59-115, 1981.

Heilmeier, H., Whale, D.M.: Carbon dioxide assimilation in the flowerhead of *Arctium*. - Oecologia **73**: 109-115, 1987.

Logan, B.A., Barker, D.H., Demmig-Adams, B., Adams, W.W., III: Acclimation of leaf carotenoid composition and ascorbate levels to gradients in the light environment within an Australian rainforest. - Plant Cell Environ. **19**: 1083-1090, 1996.

Luthra, Y.P., Sheoran, I.S., Singh, R.: Photosynthetic rates and enzyme activities of leaves, developing seeds and pod-wall of pigeon pea (*Cajanus cajan* L.). - Photosynthetica **17**: 210-215, 1983.

Schindler, C., Lichtenthaler, H.K.: Is there a correlation between light-induced zeaxanthin accumulation and quenching of variable chlorophyll *a* fluorescence? - Plant Physiol. Biochem. **32**: 813-823, 1994.

Schindler, C., Reith, P., Lichtenthaler, H.K.: Differential levels of carotenoids and decrease of zeaxanthin cycle performance during leaf development in a green and an aurea variety of tobacco. - J. Plant Physiol. **143**: 500-507, 1994.

Schreiber, U., Schliwa, U., Bilger, W.: Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. - Photosynth. Res. **10**: 51-62, 1986.

Vemmos, S.N., Goldwin, G.K.: Stomatal and chlorophyll distribution of Cox's Orange Pippin apple flowers relative to other cluster parts. - Ann. Bot. **71**: 245-250, 1993.

Vemmos, S.N., Goldwin, G.K.: The photosynthetic activity of Cox's Pippin apple flowers in relation to fruit setting. - Ann. Bot. **73**: 385-391, 1994.

Vu, J.C.V., Yelonosky, G., Baushcr, M.G.: Photosynthetic activity in the flower buds of "Valencia" orange (*Citrus sinensis* [L.] Osbeck). - Plant Physiol. **78**: 420-423, 1985.

Wardlaw, I.F.: The control of carbon partitioning in plants. - New Phytol. **116**: 341-381, 1990.

Weiss, D., Schönfeld, M., Halevy, A.H.: Photosynthetic activities in the *Petunia* corolla. - Plant Physiol. **87**: 666-670, 1988.

Wellburn, A.R.: The spectral determination of chlorophylls *a* and *b* as well as total carotenoids, using various solvents with spectrophotometers of different resolution. - J. Plant Physiol. **144**: 307-313, 1994.

Werk, K.S., Ehleringer, J.R.: Photosynthesis by flowers in *Encelia farinosa* and *Encelia californica* (*Asteraceae*). - Oecologia **57**: 311-315, 1983.

Williams, K., Koch, G.W., Mooney, H.A.: The carbon balance of flowers of *Diplacus aurantiacus* (*Scrophulariaceae*). - Oecologia **66**: 530-535, 1985.

Yong, J.W.H., How, C.S.: The patterns of photoasssimilate partitioning within connected shoots for the thin-leaved sympodial orchid *Oncidium* Goldiana during different growth stages. - Lindleyana **10**: 92-108, 1995.