Diurnal CO₂ Assimilation Patterns in Nine Species of CAM-Type Succulent Plants

Sang Deok Lee and Soon Jae Kim

Cactus Research Institute, Gyeonggi ARES, Goyang 411-809, Korea

Seung Il Jung and Ki-Cheol Son¹

Department of Environmental Science, Konkuk University, Seoul 143-701, Korea

Stanley J. Kays

Department of Horticultural Science, The University of Georgia, Athens, GA 30602-7273

Additional index words. indoor environment, volatile organic compounds

Abstract. CO₂ assimilation rate of *Crassula* hybrid 'Himaturi', a succulent ornamental species with the crassulacean acid metabolism (CAM) photosynthetic pathway, was affected by light intensity (50, 100, 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), photoperiod (16/8, 8/16 h day/night), and temperature (30/25, 25/20 °C day/night). Maximum assimilation of CO₂ occurred at 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of diurnal irradiance, 16/8 h day/night photoperiod, and a day/night temperature of 30/25 °C. Diurnal CO₂ assimilation patterns of nine succulent ornamental CAM species were evaluated (300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 35/25 °C day/night and a 16/8-h day/night photoperiod) for CO₂ fixation. Of the nine ornamentals, *Crassula* 'Himaturi' had the highest and *Echeveria derenbergii* the lowest maximum CO₂ absorption rate (13.0 vs 2.4 $\mu\text{mol}\cdot\text{kg}^{-1}\cdot\text{s}^{-1}$), total nighttime (179.3 vs 13.4 $\text{mmol}\cdot\text{kg}^{-1}$), and 24 h total (200.6 vs 19.0 $\text{mmol}\cdot\text{kg}^{-1}$) absorption. Based on the CO₂ assimilation patterns, the nine ornamentals were separated into two groups: 1) full CAM (*Faucaria tigrina*, *Gasteria gracilis* var. *minima*, *Haworthia cymbiformis*, and *Haworthia fasciata*); and 2) weakly CAM (*Adromischus clarifolius*, *Crassula* hybrids 'Moonglow' and 'Himaturi', *E. derenbergii*, and *Haworthia retusa*).

Of the three primary photosynthetic carbon fixation pathways [C₃, C₄, and crassulacean acid metabolism (CAM)], CAM species are unique in that their stomata are closed during the day, an adaptive advantage minimizing water loss in hot, dry environments. CAM plants fix carbon during the night when their stomata are open rather than during the day like in C₃ and C₄ species. Carbon dioxide is fixed through the action of phosphoenolpyruvate carboxylase, forming oxaloacetate from phosphoenolpyruvate. During the day when the stomata are closed, malate formed from oxaloacetate is decarboxylated and the CO₂ refixed through the reductive pentose phosphate cycle (Borland et al., 2000; Markovska, 1999; Mazen, 2000). Therefore, both the C₃ and C₄ cycles are operative and found within the same cells.

Only ≈6% of higher plants are CAM species (i.e., ≈16,000) (Winter and Smith, 1996), which are distributed across five taxonomic classes, 33 families, and 328 genera (Smith and Winter, 1996). Included within these are members of the Crassulaceae

as well as many cacti and succulents, some of which are important ornamental crops (Anderson, 2001). Considering the relatively large number of CAM species, there have been relatively few detailed photosynthetic studies when contrasted with C₃ and C₄ species.

The pattern of CO₂ assimilation in CAM species can be strongly modulated by environmental conditions such as light intensity, day and night temperature, daylength (Brulfert et al., 1982; Grams and Thiel, 2002; Kaplan et al., 1976a, 1976b; Lee et al., 2003a; Neales and Hew, 1975; Ota et al., 1991), water status, and mineral nutrition (Mattos and Lüttge, 2001; Ota, 1987). Although there are differences among the species, CAM plants tended to assimilate more CO₂ when grown under high light intensity (Kaplan et al., 1976a, 1976b), extended daylengths (Gregory et al., 1954), and at a nighttime temperature range between 10–22 °C (Drennan and Nobel, 2000). For example, the maximum CO₂ assimilation rate in cactus was at a 16/8-h day/night (D/N) photoperiod, 30/20 °C (D/N) temperature, and at an irradiance of 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Lee et al., 2003b).

In addition to their ornamental value, interest in the use of CAM plants in interiorscapes arises in part from their potential for removing volatile air pollutants (Son, 2004;

Woolverton et al., 1984, 1989) that build up within energy-efficient buildings, often reaching concentrations of five to seven times that of outdoor city air (Brown, 1997; Brown et al., 1994). Over 300 volatile organic compounds have been detected as indoor contaminants in addition to dust and inorganic gases (American Conference of Government and Industrial Hygienists, 1994). Volatile pollutants originating from inanimate objects (e.g., formaldehyde from carpet) within the dwelling are continuously released; however, most indoor plants are C₃ or C₄ species, which do not have their stomata open at night. CAM plants, in contrast, absorb CO₂ and other gases during the night and therefore could potentially reduce the ambient concentration of these compounds during that period. For example, *Spathiphyllum wallisii* Hort. (C₃) and *Gymnocalycium baldianum* Speg. (CAM) have comparable CO₂ exchange rates per unit surface area during the day (C₃) vs. night (CAM) (Son, 2004); thus, each would have a comparable effect on repressing the buildup of CO₂ and possibly other gases. The utilization of CAM species in interiorscapes, in addition to traditional C₃ or C₄ species, therefore, could more effectively improve indoor air quality and the well-being of people within the environment.

As a result of the number and importance of ornamental CAM species in international trade, their potential value in modulating indoor air quality, and the very limited amount of information currently available on them, our objective was to assess the CO₂ assimilation patterns and a cross-section of CO₂ absorption characteristics of nine succulent ornamentals under uniform conditions characterizing their CAM response.

Materials and Methods

Nine succulent CAM ornamentals were evaluated: *Adromischus clavifolius* Lem., *Crassula* hybrids 'Himaturi' and 'Moonglow', *Echeveria derenbergii* J.A. Purpus, *Faucaria tigrina* Schwant., *Gasteria gracilis* Baker var. *minima*, *Haworthia cymbiformis* (Haw.) Duv., *Haworthia fasciata* (Willd.) Haw., and *Haworthia retusa* (L.) Haw., each of which are popular, commercially available plants in South Korea. One-year-old, vegetatively propagated plants grown under normal glasshouse conditions (800–1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, irrigated two to three times/wk) were used. Individual plants were transplanted into 11-cm-diameter × 18-cm-tall pots containing a medium of coarse sand (1–3 mm-dia) and pig manure compost (1:1) and acclimatized ≥1 mo in a controlled-environment room maintained at 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ diurnal irradiance, 23–25 °C temperature, 40% to 60% RH, and 16/8 h (day/night) photoperiod along with 300 mL of top irrigation per 2 wk.

As a result of the unique morphology of the plants that made leaf chambers not a viable option, CO₂ exchange was measured using five constructed gas-tight cylindrical acrylic chambers (200 mm × 120-mm

Received for publication 27 Feb. 2006. Accepted for publication 24 Apr. 2006. This research was funded by a grant from Konkuk University.

¹To whom reprint requests should be addressed; e-mail kskon@konkuk.ac.kr.

diameter) designed to hold a single plant. Air was metered into the chambers at 600 mL·min⁻¹ from a cylinder containing 480 µL·L⁻¹ CO₂ and exited through an exhaust line. The differential in CO₂ concentration was automatically determined using an IR CO₂ analyzer (MC-DA CO₂ Analyzer Unit, Koito, Japan). Carbon dioxide assimilation was determined for 12 min·h⁻¹ for each chamber using solenoid switching valves controlled by a CO₂-monitoring software system (VisiDaq Tool; Advantech, Seoul, Korea). The chambers were held in a controlled-environment room; chamber temperature was modulated by altering the room temperature. All plants were irrigated 1 d before CO₂ measurement.

Photosynthetic rate was initially calculated for 'Himaturi' using leaf surface area with the leaf area determined using a Li-COR leaf area meter (LI-COR Bioscience, Lincoln, Neb.). As a result of the morphology of many of the species tested, subsequent photosynthetic rate measurements were based on the dry weight of the aerial portion of the plant (Katou et al., 1981; Lee et al., 2003b; Oomasa et al., 1992) using the following equation:

$$p = \frac{C_r - C_s}{10^6} \times F \times 60 \times \frac{273}{273 + T} \times \frac{44}{22.4} \times \frac{10}{g}$$

where p = photosynthetic rate (mg CO₂·g dwt⁻¹·h⁻¹), C_r = CO₂ input concentration (µL·L⁻¹), C_s = CO₂ exhaust concentration

(µL·L⁻¹), F = air flow rate (mL·min⁻¹), T = temperature (°C), and g = dry weight of the aerial plant parts (g). Rate was subsequently converted to µmol CO₂·kg⁻¹·s⁻¹. Dry weights were determined after oven drying at 105 °C for 8 h followed by 80 °C for 72 h.

The CO₂ assimilation measurement system allowed monitoring five chambers simultaneously (Lee et al., 2003b), four with plants and the fifth containing a control pot with media alone (i.e., above- and below-ground plant parts removed). The small amount of CO₂ uptake by the control chamber was subtracted from the plant-assimilation rates. Four replicates of each species were measured; to minimize the effect of outliers and to maintain a uniform sample size, the three most representative plants were averaged for the illustrations. To ascertain the effect of irradiance, photoperiod, and temperature on CO₂ assimilation, *Crassula* hybrid 'Himaturi' plants were initially assessed at varying light irradiances [50, 100, and 300 µmol·m⁻²·s⁻¹ (400 W metal halide lamp)], photoperiods [16/8 and 8/16 h (D/N)], and temperatures [30/25 and 25/20 °C (day/night)]. Environmental treatments were randomly assigned and the plants were allowed to equilibrate to changes in conditions for 24 h before measurement. Longer equilibration times gave comparable results. Subsequently, each of the ornamentals was tested under the environmental conditions that gave the highest CO₂-assimilation rate for 'Himaturi' [i.e., 300 µmol·m⁻²·s⁻¹ irradiance, 16/8-h (day/night) photoperiod] to allow making comparisons under uniform rather than optimum condi-

tions for each species. Several million ornamental cactus plants are sold each year as indoor plants in Korea. These are typically placed on windowsills with light intensities comparable to the irradiation level used. To maximize day/night differences, the day temperature was increased to 35 °C (i.e., 35/25 °C). The maximum CO₂ absorption rate, CO₂ absorption during the day (16 h) and night (8 h) periods, and total CO₂ absorption during 24 h and the average day and night absorption rates for each ornamental was determined. Data were analyzed by analysis of variance using standard software (SAS Institute, Cary, N.C.) with the means separated using Duncan's test.

Results and Discussion

The effect light intensity, daylength, and day/night temperature on CO₂ assimilation by *Crassula* hybrid 'Himaturi' indicated that the highest light intensity (300 µmol·m⁻²·s⁻¹) coupled with the longer photoperiod (16/8 h) and higher day temperature (30/25 °C) gave the highest rate of CO₂ uptake (Fig. 1A). Carbon dioxide assimilation was lowest when the light intensity was 50 µmol·m⁻²·s⁻¹, the photoperiod 8/16 h (day/night), and day/night temperatures 30/25 °C (Fig. 1K). As the light intensity during the daytime decreased from 300 to 50 µmol·m⁻²·s⁻¹ (Fig. 1A–D, E–H, I–L), the maximum CO₂ uptake progressively decreased. A similar response was reported for *Kalanchoe daigremontiana* Hamet. et Perr., i.e., dark CO₂ fixation

Fig. 1. Diurnal patterns of CO₂ assimilation rate as affected by light intensity (50, 100, and 300 µmol·m⁻²·s⁻¹), photoperiod (16/8 and 8/16 h day/night), and temperature (30/25 and 25/20 °C day/night) in *Crassula* hybrid 'Himaturi'. Solid bars indicate the dark period.

increased as light intensity increased (Kaplan et al., 1976a, 1976b).

The length of the light period also had a significant effect on CO₂ assimilation. The 16/8-h photoperiod at 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ resulted in a much more rapid increase in CO₂ fixation at the onset of the night period (Fig. 1A, B) than did the shorter photoperiod (8/16 h) at the same light intensity (Fig. 1C, D). The higher the light intensity, the more pronounced the response. At 50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 8/16-h photoperiod, CO₂ assimilation was exceedingly low (Fig. 1K, L). The shorter light period (8 h) also resulted in a pronounced delay in the onset of CO₂ fixation regardless of the light intensity (Fig. 1C, D, G, H, K, L). Typically, 3–4 h passed before there was a significant increase in fixation and the rate tended to decrease gradually before the end of the dark period. The influence of photoperiod on CO₂ assimilation has also been shown in the CAM species *K. daigremontiana* (Marcelle, 1975) and cactus (Lee et al., 2003a). High night temperature tended to reduce CO₂ assimilation (Fig. 1A, B) as documented in other CAM species (Neales and Hew, 1975). Maximum CO₂ assimilation occurred at 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 16/8 (day/night) photoperiod, and 30/25 °C (day/night) temperature. To maximize day/night differences, the daytime temperature was increased to 35 °C for the subsequent experiments.

The ornamentals tested had very low CO₂ assimilation during the light period, which increased markedly with the transition to the dark period (Fig. 2). Each of the species exhibited to varying degrees the classic CAM CO₂ assimilation pattern in which the four phases (Osmond, 1978) were apparent (Fig. 2A). There were, however, distinct differences among species in magnitude and timing of the onset of fixation with the start of the dark period. Neales and Hew (1975) separated plants into four categories (non-CAM, weak CAM, full CAM, and super-CAM) based on the diurnal CO₂ assimilation kinetics. Using their criteria, we found *F. tigrina*, *G. gracilis*, *H. cymbiformis*, and *H. fasciata* were in the full CAM category, which has a rapid increase in CO₂ assimilation at the onset and a maximum uptake by the midpoint of the dark period (Fig. 2). *A. clarifolius*, *Crassula* hybrids 'Moonglow' and 'Himaturi', *E. derenbergii* and *H. retusa*, in contrast, were categorized as weakly CAM species in that the increase in CO₂ assimilation was delayed until around the midpoint of the dark period and did not reach a maximum until the end of the period.

Absorption of CO₂ was further analyzed by comparing the maximum rate during the dark period, total absorption during the day, night and total day–night period (24 h), and the average rate of absorption during the day and night for each of the species (Table 1). *Crassula* hybrid 'Himaturi' displayed the highest maximum CO₂ absorption rate during the dark (i.e., 13 $\mu\text{mol}\cdot\text{kg}^{-1}\cdot\text{s}^{-1}$), whereas *H. retusa* and *E. derenbergii* had the lowest rates (i.e., 3.0 and 2.4 $\mu\text{mol}\cdot\text{kg}^{-1}\cdot\text{s}^{-1}$, respec-

Fig. 2. Diurnal CO₂ assimilation rates at 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 16/8 h day/night photoperiod, and 35/25 °C day/night temperature for: (A) *Faucaria tigrina*, (B) *Gasteria gracilis*, (C) *Haworthia cymbiformis*, (D) *Haworthia fasciata*, (E) *Adromischus clavifolius*, (F) *Crassula* hybrid 'Moonglow', (G) *Echeveria derenbergii*, (H) *Haworthia retusa*, and (I) *Crassula* hybrid 'Himaturi'. Horizontal bars indicate the dark period; vertical bars indicate the standard deviation.

tively) (Fig. 2A, Table 1). Daytime absorption of CO₂ was limited and differences among species were not statistically significant. The percentage of daytime relative to nighttime absorption was generally small, however, when absorption during the night was low, daytime absorption made up a cor-

respondingly larger percent (e.g., 29.4% for *E. derenbergii*; data not shown). Average daytime CO₂ absorption rates ranged from 0.4 to 1.3 $\text{mmol}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$, whereas nighttime rates ranged from 1.7 to 22.4 $\text{mmol}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$. Differences among species in the rate of night CO₂ absorption were statistically significant

Table 1. Maximum CO₂ absorption rate, day (16 h) and night (8 h) CO₂ absorption and absorption rate, and total CO₂ absorption during 24 h for nine species of ornamental house plants.

Species	Maximum CO ₂ absorption rate (μmol·kg ⁻¹ ·s ⁻¹)	Day CO ₂ absorption (mmol·kg ⁻¹)	Day CO ₂ absorption rate (mmol·kg ⁻¹ ·h ⁻¹)	Night CO ₂ absorption (mmol·kg ⁻¹)	Night CO ₂ absorption rate (mmol·kg ⁻¹ ·h ⁻¹)	Total CO ₂ absorption (mmol·kg ⁻¹)
<i>Crassula</i> 'Himaturi'	13.0 a ²	21.3	1.3	179.3 a	22.4 a	200.6 a
<i>Haworthia cymbiformis</i>	6.8 b	12.9	0.8	128.1 ab	16.0 ab	141.0 ab
<i>Faucaria tigrina</i>	5.5 bc	22.0	1.4	108.3 bc	13.5 bc	130.3 abc
<i>Crassula</i> 'Moonglow'	5.0 bc	9.0	0.6	49.1 cde	6.1 cde	58.1 bcd
<i>Haworthia fasciata</i>	4.7 bc	35.2	2.2	91.4 bcd	11.4 bcd	126.5 abc
<i>Adromischus clavifolius</i>	4.2 bc	7.5	0.5	46.5 cde	5.8 cde	54.0 bcd
<i>Gasteria gracilis</i>	3.6 bc	14.6	0.9	64.3 bcde	8.0 bcde	78.9 bcd
<i>Haworthia retusa</i>	3.0 c	7.8	0.5	33.0 de	4.1 de	40.9 cd
<i>Echeveria derenbergii</i>	2.4 c	5.6	0.4	13.4 e	1.7 e	19.0 d
Significance	**	NS	NS	*	**	*

²Mean separation within columns by Duncan's multiple range test at $P = 0.05$.

NS,*,** Nonsignificant or significant at $P < 0.05$ or $P < 0.01$, respectively.

($P = 0.01$). There were substantial differences in the total night absorption of CO₂ with *Crassula* 'Himaturi' having the highest (179.3 mmol·kg⁻¹) and *E. derenbergii* the lowest (13.4 mmol·kg⁻¹). *Crassula* 'Himaturi' and *H. cymbiformis*, had nighttime CO₂ absorption rates that were 17 to 20 times that of the daytime. A similar range was found for the total CO₂ absorption among the species tested (i.e., 200.6 mmol·kg⁻¹ for *Crassula* 'Himaturi' to 19.0 mmol·kg⁻¹ for *E. derenbergii*). *E. derenbergii* had the lowest day, night, and total CO₂ absorption with a daytime rate of only 0.4 mmol·kg⁻¹·h⁻¹ and a nighttime rate of 1.7 mmol·kg⁻¹·h⁻¹. The nighttime rate of CO₂ absorption was only ≈4× higher than during the day; in contrast, *H. cymbiformis* was 20× that of the day (data not shown). Collectively, there were substantial differences among the ornamentals tested in their CO₂ absorption ability.

Conclusions

Of the nine ornamentals, *Crassula* 'Himaturi' had the highest and *E. derenbergii* the lowest maximum CO₂ absorption rate and total nighttime and total daily CO₂ absorption. Sequestering or metabolism of certain volatile organic compounds by a number of species occurs to a significant degree through stomatal diffusion into the interior of the plant. Although facilitated gas exchange does not translate directly into the ability to remove pollutants, access to the interior is often an important component. Based on CO₂ assimilation rate and apparent stomatal response, our results indicate that *Crassula* 'Himaturi', *H. cymbiformis*, *F. tigrina*, and *H. fasciata* were the most attractive and *E. derenbergii* the least attractive candidates for subsequent analysis of their ability to remove undesirable indoor volatile organic compounds.

Literature Cited

American Conference of Government and Industrial Hygienists. 1994. Threshold limit values for chemical substances and physical agents and biological exposure indices. American

- Conference of Government and Industrial Hygienists, Cincinnati, Ohio.
- Anderson, E.F. 2001. Distinctive features of cacti. In: The cactus family. Timber Press, Portland. pp. 15–41.
- Borland, A.M., K. Maxwell, and H. Griffiths. 2000. Ecophysiology of plants with crassulacean acid metabolism. Adv. Photosynthesis 9:583–605.
- Brown, S.K. 1997. Volatile organic compounds in indoor air: sources and control. Australian Jan./Feb. pp. 10–13.
- Brown, S.K., M.R. Sim, M.J. Abramson, and C.N. Gray. 1994. Concentrations of volatile organic compounds in indoor air—A review. Indoor Air 4:123–134.
- Brulfert, J., M. Muller, M. Kluge, and O. Queiroz. 1982. Photoperiodism and crassulacean acid metabolism. Planta 154:326–331.
- Drennan, P.M. and P.S. Nobel. 2000. Responses of CAM species to increasing atmospheric CO₂ concentrations. Plant Cell Environ. 23:767–781.
- Grams, T.E.E. and S. Thiel. 2002. High light-induced switch from C₃-photosynthesis to Crassulacean acid metabolism is mediated by UV-A/blue light. J. Expt. Bot. 53:1475–1483.
- Gregory, F.G., J. Spear, and K.V. Thimann. 1954. The interrelation between CO₂ metabolism and photoperiodism in *Kalanchoe*. Plant Physiol. 29:220–229.
- Kaplan, A., J. Gale, and A. Poljakoff-Mayber. 1976a. Simultaneous measurement of oxygen, carbon dioxide, and water vapour exchange of intact plants. J. Expt. Bot. 97:214–219.
- Kaplan, A., J. Gale, and A. Poljakoff-Mayber. 1976b. Resolution of net dark fixation of carbon dioxide into its respiration and gross fixation components in *Bryophyllum daigremontianum*. J. Expt. Bot. 97:220–230.
- Katou, S., S.T. Miyachi, and Y.O. Murata. 1981. The method of photosynthesis study. Kyouritsu Pub. Corp., Tokyo.
- Lee, S.D., S.I. Jung, M.J. Kim, S.H. Kim, P.G. Kim, S.J. Kim, and K.C. Son. 2003a. Effects of light intensity, photoperiod, and night temperature on diurnal CO₂ exchange rate in cacti. J. Kor. Soc. Hort. Sci. 44:774–779.
- Lee, S.D., S.I. Jung, S.H. Kim, M.J. Kim, Y.J. Kim, K. Namkung, and K.C. Son. 2003b. Comparison of diurnal CO₂ exchange patterns in various cacti by using CO₂ exchange analysis system for whole plants. J. Kor. Soc. Hort. Sci. 44:767–773.
- Marcelle, R. 1975. Effect of photoperiod on the CO₂ and O₂ exchanges on leaves of *Bryophyllum daigremontianum*. In: Environmental and biological control of photosynthesis. In: R. Marcelle (ed.). W. Junk, The Hague. pp. 349–356.
- Markovska, Y.K. 1999. Gas exchange and malate accumulation in *Haberlea rhodopensis* grown under different irradiances. Biol. Plant. 42:559–565.
- de Mattos, E.A. and U. Lüttge. 2001. Chlorophyll fluorescence and organic acid oscillations during transition from CAM to C₃-photosynthesis in *Clusia minor* L. (Clusiaceae). Ann. Bot. (Lond.) 88:457–463.
- Mazen, A.M.A. 2000. Changes in properties of phosphoenolpyruvate carboxylase with induction of crassulacean acid metabolism (CAM) in the C₄ plant *Portulaca oleracea*. Photosynthetica 38:385–391.
- Neales, T.F. and C.S. Hew. 1975. Two types of carbon fixation in tropical orchids. Planta 123:303–306.
- Oomasa, K.J., N.A. Kondou, and Y.N. Ieue. 1992. The measurement and diagnosis of plants. Chyousou Corp., Tokyo.
- Osmond, C.B. 1978. Crassulacean acid metabolism: A curiosity in context. Ann. Rev. Plant Physiol. 29:379–414.
- Ota, K. 1987. What is CAM-type photosynthesis? Biol. Sci. 39:192–199.
- Ota, K., K. Morioka, and Y. Yamamoto. 1991. Effects of leaf age, inflorescence, temperature, light intensity and moisture conditions on CAM photosynthesis in *Phalaenopsis*. J. Jpn. Soc. Hort. Sci. 60:125–132.
- Smith, J.A.C. and K. Winter. 1996. Taxonomic distribution of crassulacean acid metabolism. In: Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. In: K. Winter and J.A.C. Smith (eds.). Springer-Verlag, Berlin. pp. 427–436.
- Son, K.-C. 2004. Indoor plants help people stay healthy. Joongang Life Pub. Co., Seoul.
- Winter, K. and J.A.C. Smith. 1996. An introduction to crassulacean acid metabolism. Biochemical principles and ecological diversity. In: Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. In: K. Winter and J.A.C. Smith (eds.). Springer-Verlag, Berlin. pp. 1–13.
- Woolverton, B.C., A. Johnson, and K. Bounds. 1989. Interior landscape plants for indoor air pollution abatement. Final Report, September N.A.S.A. 1989 Stennis Space Center, Miss.
- Woolverton, B.C., R.C. McDonald, and E.A. Watkins Jr. 1984. Foliage plants for removing indoor air pollutants from energy-efficient homes. Econ. Bot. 38:224–228.