

## Variation in photosynthetic characteristics and leaf area contributes to *Spathiphyllum* cultivar differences in biomass production

Qibing WANG and Jianjun CHEN\*

*University of Florida, IFAS, Mid-Florida Research and Education Center  
and Department of Environmental Horticulture, 2725 Binion Road, Apopka, FL 32703, USA*

### Abstract

Three genetically related *Spathiphyllum* cultivars, Claudia, Double Take, and Petite with similar initial sizes and biomass, were grown in a shaded greenhouse and fertilized with a constant supply of nitrogen at 200 g m<sup>-3</sup> using an ebb-and-flow fertigation system. Seven months later, Claudia and Double Take had plant sizes and biomasses significantly greater than Petite. Stomatal conductances of Claudia and Double Take were 30 % greater, thus net photosynthetic rates ( $P_N$ ) were significantly higher than in Petite. In addition, the leaf areas (LA) of Claudia and Double Take were 60 % larger than of Petite. Since  $P_N$  was expressed per leaf surface area, the greater the LA was, the more CO<sub>2</sub> was fixed. Thus, the differences in plant size and biomass production of Claudia and Double Take compared to Petite are attributed to high  $P_N$  and increased LA.

*Additional key words:* biomass; chlorophyll content; intercellular CO<sub>2</sub> concentration; leaf area and thickness; net photosynthetic rate; ornamental foliage plants; peace lily; stomatal conductance; water-use efficiency.

*Spathiphyllum* Schott, commonly known as peace lily, is a member of the family Araceae native to densely shaded rainforests of the tropical Americas, Indonesia, Malaysia, and the Philippines (Bunting 1960). The plant was initially described by Jacquin (1790), later by Schott (1832), and introduced into Europe for cultivation in 1874 (Birdsey 1951). A total of 41 species have been recognized (Mayo *et al.* 1997), all of them are evergreen rhizomatous herbs. Among them, several species are prized for their unique and elegant white or creamy spathes and deep green foliage. However, *Spathiphyllum* just recently has emerged as an important ornamental foliage plant. By the end of the 1970s, there were only five cultivars in production and no records about its wholesale value in the U.S. (McConnell *et al.* 1989). There were more than 50 cultivars (Chen *et al.* 2002) with a wholesale value of \$35 million in 1998 (USDA 1999). Contemporary cultivated *Spathiphyllum* are mostly hybrids (Henny and Chen 2003) and produced in containerized soil-less substrates

under shaded environments. After attaining a marketable size, container-grown *Spathiphyllum* is sold as living specimen for interior decoration (Griffith 1998).

Environmental conditions and cultural practices for commercial production of *Spathiphyllum* have been established over the last 10 years. Conover (1992) recommended that *Spathiphyllum* should be produced under a photosynthetic photon flux density of 200 to 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and a temperature range of 20 to 32 °C. With the recent increase of new hybrids, cultivars varying in growth rates and sizes have been observed (Henny and Chen 2003).

Variation in size and biomass accumulation contributes to variation in fitness (Solbrig 1981, Arntz *et al.* 1998). Genetic variation in photosynthetic characters and biomass accumulation has been reported in various plant species (Kalisz 1986, Geber and Dawson 1997, Arntz *et al.* 1998). To our knowledge, however, photosynthetic and leaf morphological characteristics in relation to

Received 5 February 2003, accepted 14 August 2003.

\*Author for correspondence; fax: +407-814-6186, e-mail: jjchen@mail.ifas.ufl.edu

**Abbreviations:** Chl, chlorophyll;  $C_i$ , intercellular CO<sub>2</sub> concentration; DM, dry mass;  $E$ , transpiration rate; FM, fresh mass;  $g_s$ , stomatal conductance; LA, leaf area, LT, leaf thickness;  $P_N$ , net photosynthesis rate; RuBP, ribulose-1,5-bisphosphate; RuBPC, ribulose-1,5-bisphosphate carboxylase; SLA, specific leaf area; WC, water content; WUE, water-use efficiency.

**Acknowledgments:** This research was supported by the Florida Agricultural Experiment Station and approved for publication as Journal Series No. R-09504. The authors thank Kelly Everitt for critical reading of the manuscript.

*Spathiphyllum*'s biomass accumulation have not been documented. Therefore we determined leaf photosynthetic and morphological characteristics of three genetically related *Spathiphyllum* cultivars, examined the importance of these characteristics to plant size increase and biomass accumulation, and identified factors that could potentially be selection traits for improving *Spathiphyllum* growth in production.

Tissue cultured explants of *Spathiphyllum* cvs. Claudia, Double Take, and Petite, 10 weeks out of culture and rooted in 2.5-cm plastic cell trays, were obtained from *Agri-Starts*, Apopka, FL and *Twysford International*, Apopka, FL. After removal from trays, uniform single plants were planted into 15-cm diameter pots filled with *Vergo Container Mix A* (*Verlite Co.*, Tampa, FL): Canadian peat, vermiculite, and perlite (3 : 1 : 1 by vol.). All plants were randomly placed on grooved 2.4 m<sup>2</sup> ebb-and-flow trays leveled on benches in a shaded and evaporated pad cooled greenhouse under a maximum photosynthetically active radiation of 250  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Temperature ranged from 20 to 32 °C and relative humidity from 60 to 100 %.

Plants grown on the ebb-and-flow trays were sub-irrigated with a nutrient solution made from a water-soluble fertilizer 17N-2.1P-15.7K (Peters 24N-8P<sub>2</sub>O<sub>5</sub>-16K<sub>2</sub>O, *Grace-Sierra Horticultural Products*, Milpitas, CA) with micronutrients. The fertilizer was added to well water stored in closed polybutylene 75 000 cm<sup>3</sup> receptacles (*Rubbermaid*, Winchester, VA) at 1.2 kg m<sup>-3</sup> so that the N concentration was 200 g m<sup>-3</sup>. Each ebb-and-flow tray was accompanied with a receptacle in which a submersible pump was equipped. All pumps were controlled by an automatic timer, and solution was pumped into each ebb-and-flow tray to a depth of 2.5 cm for 10 min two to three times a week so that all plants received the fertigation at the same time and duration. Solutions were then permitted to drain back into the storage receptacle for continuous use. Ammonium- and nitrate-N concentrations in each receptacle were examined weekly using the methods described by Diatloff and Rengel (2001). Additional amounts of the water-soluble fertilizer were added to maintain a total N in each receptacle at 200 g m<sup>-3</sup>.

The experiment was arranged in a completely randomized design with six replications. Three weeks after transplanting (March), three replicates were randomly selected from the six and photosynthetic parameters, seedling heights and canopy widths, dry mass (DM) of shoots and roots, were measured. Four months (July) after transplanting, photosynthetic parameters of the remaining three replicates were measured. Three months later (October) canopy heights and widths, leaf characteristics, photosynthetic parameters, and chlorophyll (Chl) contents were measured. Plants were harvested and total carbon (C) and N of leaves and DM of shoots and roots were determined.

Net photosynthetic rate ( $P_N$ ), stomatal conductance

( $g_s$ ), intercellular CO<sub>2</sub> concentration ( $C_i$ ), and transpiration rate ( $E$ ) of three recent fully-expanded leaves of each plant were determined with a *LCi* portable photosynthesis system (*ADC BioScientific*, Hoddesdon, UK) between 10:00 and 14:00 under greenhouse conditions. During such measurements, the CO<sub>2</sub> concentration of reference varied from 360 to 370  $\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}(\text{air})$  within the leaf chamber, and temperature ranged from 29 to 32 °C. Gas exchange parameters were recorded when  $C_i$  attained the stable value. Ten readings were taken per leaf. Water-use efficiency (WUE) was calculated as  $P_N/E$ .

Immediately after  $P_N$  measurements, ten 0.3 cm<sup>2</sup> discs were punched from each of the three leaves, weighed, and then extracted with 5 cm<sup>3</sup> *N,N*-dimethylformamide for 72 h in the dark at 4 °C. Chl absorbance was determined using a spectrophotometer (*SmartSpec 3000*, *Bio-RAD Laboratories*, Hercules, CA) at 647 and 664 nm. The readings were used to calculate Chl *a* and *b* concentrations (Porra *et al.* 1989).

The same three leaves used for the  $P_N$  and Chl measurements were detached from petioles. Individual fresh leaves were weighed and passed through *LI-3100* Area Meter (*LI-Cor*, Lincoln, NE) for leaf area (LA) measurements. The sum of the measured LA with the corresponding 10 disc areas gave an entire LA. Each leaf was then cut into 16 pieces and these pieces were piled up, the thickness of the pile was measured using vernier calipers (Jiang *et al.* 2002). The leaves, minus the 10 discs for Chl analysis, were oven-dried for 72 h at 80 °C, and DMs were recorded. Specific leaf area (SLA) was calculated by LA divided by its DM. Dried leaves were ground to a powder for total N and C analyses by a *CNS Auto-Analyzer* (*VarioMAX*, *Elementar Americas*, Mt Laurel, NJ). Shoots were excised at the surface of container substrate. Roots were washed with de-ionized water to remove container substrate. After determining fresh masses (FM), shoots and roots were oven-dried at 80 °C for 72 h, and DMs were measured. Total shoot DM of each plant was the sum of the DM of the three excised leaves with that of the remaining shoots.

Measured parameters were analyzed using the *PROC GLM* procedure of the *SAS* statistical software package (*SAS Institute*, Cary, NC). If significant differences existed among cultivars, means were separated by Duncan's multiple range test at 5 % level. Additionally, Pearson's correlation analysis was performed to assess the relationship among some measured characteristics, and linear models were established for significantly correlated parameters using *SigmaPlot 2000* (*Jandel Scientific Software*, San Rafael, CA).

The three cultivars initially did not differ in size and biomass, which was illustrated by their heights and widths, and shoot, root, and total DMs (Table 1). However,  $P_N$ ,  $g_s$ ,  $C_i$ , and  $E$  of Claudia and Double Take varied significantly from Petite (Table 1). Due to its low  $E$ , however, WUE of Petite was significantly higher than

Table 1. Net photosynthetic rate,  $P_N$  [ $\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ ], stomatal conductance,  $g_s$  [ $\text{mol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$ ], intercellular  $\text{CO}_2$  concentration,  $C_i$  [ $\text{cm}^3 \text{ m}^{-3}$ ], transpiration rate,  $E$  [ $\text{mmol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$ ], and water use efficiency, WUE [ $\text{mmol}(\text{CO}_2) \text{ mol}^{-1}(\text{H}_2\text{O})$ ] of three recently fully expanded leaves as well as plant canopy height and width, and shoot, root, and total dry masses (DM) of *Spathiphyllum* cultivars Claudia, Double Take, and Petite measured three weeks (21 d) or seven months (212 d) after transplanting (October 2002). Means of nine leaves (three leaves per replicate) for  $P_N$ ,  $g_s$ ,  $C_i$ ,  $E$ , and WUE; for other characteristics means of three containerized plants. Means of each age group followed by different letters within columns were significantly different based on Duncan's multiple range test at 5 % level.

Cultivar	Age [d]	Canopy height	width	DM [g]			$P_N$	$g_s$	$C_i$	$E$	WUE
				shoot	root	total					
Claudia	21	11.52a	10.25a	0.09a	0.04a	0.13a	4.07a	0.13a	303.50a	2.88b	1.48b
Double Take		11.28a	10.46a	0.09a	0.04a	0.13a	4.18a	0.14a	299.88a	3.65a	1.17c
Petite		11.26a	10.54a	0.09a	0.03a	0.12a	3.16b	0.05b	221.82b	1.21c	2.77a
Claudia	212	57.02a	50.05a	50.13a	14.88a	65.01a	5.20a	0.25a	303.98a	3.72a	1.42a
Double Take		54.76a	56.76a	48.57a	14.19a	62.76a	5.19a	0.29a	311.08a	3.68a	1.43a
Petite		43.48b	45.94b	31.72b	13.31b	45.03c	4.62b	0.19b	305.96a	3.20b	1.48a

that of the other two cultivars. The lower  $P_N$  at this early growth stage of Petite was probably attributed to its low  $g_s$  since it was two times less than either Claudia or Double Take. Stomatal limitation (low  $g_s$ ) has been considered to decrease  $P_N$ ,  $C_i$ , and  $E$  (Wong *et al.* 1979, Farquhar and Sharkey 1982, Geber and Dawson 1997) that thus inhibits metabolism.

As three cultivars' growth under the controlled environment and fertilized with a constant supply of N at an optimal rate continued, plant differences in size and biomass accumulation became apparent seven months later (Table 1). The height and width of Petite was 18 and 17 % less than those of Claudia and Double Take, respectively. Total DM of Petite was 28 % less than that of either Claudia or Double Take. The small size and low biomass of Petite was probably due in part to the significantly lower  $g_s$  and subsequently lower  $P_N$  than Claudia and Double Take since  $g_s$  and  $P_N$  are significantly correlated:  $y = 4.156 + 3.396 x$ ;  $r = 0.521$  at  $p = 0.05$ . However, the  $C_i$  of Petite measured in October did not significantly differ from that of the other two cultivars. We speculate that the lower  $P_N$  in Petite, in addition to stomatal limitation, may also relate to biochemical limitation. Two important sources have been considered for the biochemical limitation: one is the limitation of RuBPC activity of mesophyll cells and the other the regeneration of RuBP during electron transport (Sharkey 1985, Woodrow and Berry 1988).

The magnitudes of  $P_N$  and  $g_s$  measured in October were similar to those measured in July (values not shown) but different from those measured in March (Table 1) regardless of cultivars. The  $g_s$  measured in March were nearly 50 % less than those measured in October. Accordingly,  $P_N$  measured in March were lower than in October. Both seasonal and age-related changes in photosynthesis have been documented in various plant species (Hajra and Kumar 1999, Bond 2000, Mackenzie *et al.* 2001). The differences in  $g_s$  and  $P_N$  in *Spathiphyllum*

are likely plant age and season related even though plants were cultivated under a controlled environment.

Further characterization of the three recently fully-expanded leaves showed that total N and C contents and Chl *a* and *b* contents were not significantly different among cultivars (Table 2), suggesting that N, C, and Chl contents were not causes of the cultivar difference in photosynthesis. Since  $P_N$  in both Claudia and Double Take were higher than Petite, the mean FMs and DMs of the three individual leaves were significantly greater than those of Petite. SLA among three leaves of each cultivar was rather constant (with standard errors of Claudia, Double Take, and Petite were 0.64, 0.41, and 0.46, respectively), which proved that the three leaves were fully expanded (Gratani and Ghia 2002). However, SLA of Claudia was significantly lower than that of the other two cultivars. This is probably linked to its lower leaf water content than in Double Take and Petite (Table 2). The three cultivars had almost identical leaf thickness (LT), suggesting little difference in mesophyll resistance among the three cultivars. Nobel (1991) believed that the greater LT could result in increased mesophyll resistance, which then limits  $\text{CO}_2$  influx to the sites of carboxylation and thus reduces  $P_N$ . Among the leaf characters measured, mean LA was probably the most importantly morphological parameter that was a major contributor to the great difference in biomass production. Mean LA of Petite was almost 60 % less than that of Claudia and Double Take (Table 2). Mean total leaf numbers per plant were not significantly different among cultivars: 54, 55, and 55 for Claudia, Double Take, and Petite, respectively. Since  $P_N$  was expressed per leaf surface area, the greater the LA was, the more  $\text{CO}_2$  was fixed. Thus, the increased plant sizes and DMs in Claudia and Double Take are attributed to two factors, high  $P_N$  and increased LA.

Petite has been one of the most common cultivars in commercial production for more than two decades, but Claudia and Double Take were recently patented and

Table 2. Characteristics of three recently fully expanded leaves of *Spathiphyllum* cultivars Claudia, Double Take, and Petite at the end of experiment (October 2002). DM = dry mass; FM = fresh mass; LA = leaf area; LT = leaf thickness; SLA = specific leaf area; WC = water content. Means of nine leaves (three leaves per replicate); those followed by different letter within columns were significantly different based on Duncan's multiple range test at 5 %.

Cultivar	DM	FM	WC	LA	SLA	LT	N	C	Chl [ $\mu\text{mol m}^{-2}$ ]		
	[g]	[g]	[%]	[ $\text{cm}^2$ ]	[ $\text{m}^2 \text{kg}^{-1}$ ]	[mm]	[%]	[%]	<i>a</i>	<i>b</i>	<i>a+b</i>
Claudia	0.88a	5.31a	489.05c	196.35a	22.70b	0.23a	3.40a	43.25a	61.04a	51.98a	113.03a
Double Take	0.71b	4.68b	571.46a	181.12a	25.81a	0.23a	3.42a	43.07a	61.87a	55.72a	117.59a
Petite	0.46c	3.29c	560.07a	114.20b	25.17a	0.24a	3.58a	44.13a	59.94a	49.18a	109.12a

released hybrids (U.S. plant patent Nos. 10,893 and 12,835, respectively). Although they were developed from their respective cross of two different parents, both Claudia and Double Take have one fourth of their genetic makeup derived from Petite, suggesting that three of them are genetically related. However, their differences in size and biomass accumulation suggest that growth habit of *Spathiphyllum* can be genetically improved through breeding. The identified factors, high  $g_s$ ,  $P_N$ , and LA, could be used as indicators for early selection of progenies with high biomass production, thus large plant sizes. For example, the consistency of high  $g_s$  and corresponding

high  $P_N$  between their early and late growth stages in Claudia and Double Take could be important parameters for identifying parents to make crosses and for selecting progenies from crosses. In fact, Percy *et al.* (1996) showed a clear-cut genetic regulation of  $g_s$  in Pima cotton (*Gossypium barbadense*), and Lu *et al.* (1998) proposed that high  $g_s$  could be used as selection trait for high yields. With increased understanding of physiological and morphological aspects of *Spathiphyllum* productivity, this rainforest understory originated ornamental could be better improved in both size and biomass production.

## References

Arntz, A.M., Delucia, E.H., Jordan, N.: Contribution of photosynthetic rate to growth and reproduction in *Amaranthus hybridus*. – *Oecologia* **117**: 323-330, 1998.

Birdsey, M.R.: The Cultivated Aroid. – Gillick Press, Berkeley 1951.

Bond, B.J.: Age-related changes in photosynthesis of woody plants. – *Trends Plant Sci.* **5**: 349-353, 2000.

Bunting, G.S.: A revision of *Spathiphyllum* (Araceae). – *Mem. New York bot. Gard.* **10**: 1-54, 1960.

Chen, J., Henny, R.J., McConnell, D.B.: Development of new foliage plant cultivars. – In: Janick, J., Whipkey, A. (ed.): *Trends in New Crops and New Uses*. Pp. 446-452. ASHS Press, Alexandria 2002.

Conover, C.A.: Foliage plants. – In: Larson, R.A. (ed.): *Introduction to Floriculture*. Pp. 569-601. Academic Press, New York 1992.

Diatloff, E., Rengel, Z.: Compilation of simple spectrophotometric techniques for the determination of elements in nutrient solutions. – *J. Plant Nutr.* **24**: 75-86, 2001.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. – *Annu. Rev. Plant Physiol.* **33**: 317-345, 1982.

Geber, M.A., Dawson, T.E.: Genetic variation in stomatal and biochemical limitation to photosynthesis in the annual plant, *Polygonum arenastrum*. – *Oecologia* **109**: 535-546, 1997.

Gratani, L., Ghia, E.: Changes in morphological and physiological traits during leaf expansion of *Arbutus unedo*. – *Environ. exp. Bot.* **48**: 51-60, 2002.

Griffith, L.P.: Tropical Foliage Plants: A Growers Guide. – Ball Publishing, Batavia 1998.

Hajra, N.G., Kumar, R.: Seasonal variation in photosynthesis and productivity of young tea. – *Exp. Agr.* **35**: 71-85, 1999.

Henny, R.J., Chen, J.: Cultivar development of ornamental foliage plants. – *Plant Breeding Rev.* **23**: 245-290, 2003.

Jacquin, N.J.: Araceae. – In: *Collectanea ad Botanicam, Chemiam, Historiam Naturalem Spectantia, cum Figuris*. Vienna 1790.

Jiang, H., Wang, X.-H., Deng, Q.-Y., Yuan, L.-P., Xu, D.-Q.: Comparison of some photosynthetic characters between two hybrid rice combinations differing in yield potential. – *Photosynthetica* **40**: 133-137, 2002.

Kalisz, S., Teeri, J.A.: Population-level variation in photosynthetic metabolism and growth in *Sedum wrightii*. – *Ecology* **67**: 20-26, 1986.

Lu, Z., Percy, R.G., Qualset, C.O., Zeiger, E.: Stomatal conductance predicts yields in irrigated Pima cotton and bread wheat grown at high temperatures. – *J. exp. Bot.* **49**: 453-460, 1998.

Mackenzie, T.D.B., MacDonald, T.M., Dubois, L.A., Campbell, D.A.: Seasonal changes in temperature and light drive acclimation of photosynthetic physiology and macromolecular content in *Lobaria pulmonaria*. – *Planta* **214**: 57-66, 2001.

Mayo, S.J., Bogner, J., Boyce, P.C.: The Genera of Araceae. – Royal Botanic Garden, Kew 1997.

McConnell, D.B., Henley, R.W., Kelly, C.B.: Commercial foliage plants: Twenty years of changes. – *Proc. Florida State hortic. Soc.* **102**: 297-303, 1989.

Nobel, P.S.: *Physiochemical and Environmental Plant Physiology*. – Academic Press, San Diego 1991.

Percy, R.G., Lu, Z., Radin, J.W., Turcotte, E.I., Zeiger, E.: Inheritance of stomatal conductance in cotton (*Gossypium barbadense*). – *Physiol. Plant.* **96**: 389-394, 1996.

Porra, R.J., Thompson, W.A., Kriedemann, P.E.: Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls *a* and *b* extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. – *Biochim. biophys. Acta* **975**: 384-394, 1989.

Schott, H.W.: Araceae. – In: Schott, H.W., Endlicher, S.: *Meletemata Botanica*. Pp. 16-22. C. Gerold, Vienna 1832.

Sharkey, T.D.: Photosynthesis in intact leaves of C<sub>3</sub> plants: physics, physiology and rate limitations. – *Bot. Rev.* **51**: 53-105, 1985.

Solbrig, O.T.: Studies on the population biology of the genus *Viola*. II. The effect of plant size on fitness in *Viola sororia*. – *Evolution* **35**: 1080-1093, 1981.

USDA (United States Department of Agriculture): *Floriculture Crops 1998 Summary*. – USDA, Washington 1999.

Wong, S.C., Cowan, I.R., Farquhar, G.D.: Stomatal conductance correlates with photosynthetic capacity. – *Nature* **282**: 424-426, 1979.

Woodrow, I.E., Berry, J.A.: Enzymatic regulation of photosynthetic CO<sub>2</sub> fixation in C<sub>3</sub> plants. – *Annu. Rev. Plant Physiol. Plant mol. Biol.* **39**: 533-594, 1988.