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# Functional relationship between leaf/stem pseudobulb size and photosynthetic pathway in the Orchidaceae

Zhenzhu Fu, Craig E. Martin, Jeney Do, Che-Ling Ho, and Babs Wagner

**Abstract:** Water storage has been commonly cited as an important function of orchid pseudobulbs, and it is reasonable to assume that orchids which utilize crassulacean acid metabolism (CAM) photosynthesis have larger pseudobulbs than those of  $C_3$  orchid taxa, because these foliar (or stem) structures may reflect another type of succulent tissue in CAM plants. On the other hand, it is equally plausible that  $C_3$  orchids have larger pseudobulbs, as they lack succulent tissue, as well as the water-conservative CAM pathway. The goal of this study was to compare pseudobulb size in over 100 living orchid species growing at the Missouri Botanical Garden by measurement. Pseudobulb volumes of  $C_3$  species did not differ from those of species with CAM photosynthesis in a family-wide comparison of all sampled species, as well as in comparisons of taxa with these two photosynthetic pathways among three subtribes and within one genus. The results did not support a functional relationship between pseudobulb volume and photosynthetic pathway in the Orchidaceae. Pseudobulbs are equally important structures in  $C_3$  and CAM orchid taxa, and may function similarly in water, carbohydrates, and (or) essential elements storage in the two groups of orchids. This study lays a foundation for further research into pseudobulb evolution in orchids.

**Key words:**  $C_3$  photosynthesis, crassulacean acid metabolism,  $\delta^{13}C$ , ecophysiology, leaf morphology, orchids, stem morphology, succulence, water storage.

**Résumé :** On a souvent mentionné que le stockage d'eau est une importante fonction des pseudo-bulbes de l'orchidée et il est raisonnable de supposer que les orchidées illustrant le métabolisme acide des Crassulacées (MAC) possèdent de plus gros pseudo-bulbes que celles qui fixent le carbone en  $C_3$ , car ces structures de la feuille (ou de la tige) pourraient constituer une forme de tissu succulent chez les plants MAC. D'un autre côté, il se pourrait aussi que les orchidées  $C_3$  aient de plus gros pseudo-bulbes parce qu'elles sont privées de tissus succulents et de la voie MAC pour économiser l'eau. Les auteurs voulaient comparer la taille des pseudo-bulbes d'une centaine d'espèces d'orchidées poussant au jardin botanique du Missouri. Les orchidées  $C_3$  ont des pseudo-bulbes d'un volume identique à ceux des espèces photosynthétiques MAC. C'est ce que révèle la comparaison des espèces échantillonnées par famille ainsi que la comparaison des taxons de trois sous-tribus et d'un genre possédant les deux voies de photosynthèse. Les résultats ne vont pas dans le sens d'une relation fonctionnelle entre le volume des pseudo-bulbes et la voie de la photosynthèse chez les Orchidacées. Le pseudo-bulbe revêt autant d'importance chez les taxons  $C_3$  que chez les taxons MAC et pourrait fonctionner de la même manière en stockant l'eau, les hydrates de carbone ou des substances essentielles chez les deux groupes. Cette étude pave la voie à des recherches plus poussées sur l'évolution du pseudo-bulbe chez l'orchidée. [Traduit par la Rédaction]

**Mots-clés :** photosynthèse en  $C_3$ , métabolisme acide des Crassulacées,  $\delta^{13}C$ , écophysologie, morphologie de la feuille, orchidées, morphologie de la tige, succulence, stockage de l'eau.

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## Introduction

The Orchidaceae is a highly diverse and widespread monocotyledonous family of flowering plants, and it is the largest vascular plant family on earth, comprising about 800 genera and likely more than 28 000 species worldwide (Fay and Chase 2009; Christenhusz and Byng 2016). Because many orchids, especially tropical species, have such narrow niches and limited distributions, the actual number of species is unknown. The incomplete knowledge of the number of tropical species is due, in part, to the limited collection data in areas of poor accessibility. Orchids are either epiphytic or terrestrial, and the photosynthetic pathway of Orchidaceae taxa includes both the  $C_3$  and crassulacean acid metabolism (CAM) photosynthetic pathways (Neales and Hew 1975; Avadhani et al. 1978, 1981, 1982; Hew and Yong 1997; Silvera et al. 2005, 2009, 2010a, 2010b). For example, an investigation of  $\delta^{13}C$  values of 1002 orchid species originating from Panama and Costa Rica revealed that over 90% of the species were  $C_3$  plants, while the remainder exhibited the CAM photosynthetic pathway (Silvera et al. 2010b). Other studies indicate that CAM orchids may comprise a greater proportion (e.g., up to 50%) of orchid taxa sampled in an area or collection (Winter et al. 1983; Silvera et al. 2005, 2009), especially if a more inclusive definition of CAM photosynthesis is used (e.g., including forms of  $C_3$ -CAM intermediacy, such as CAM-cycling; Martin et al. 1988; Martin 1996; Herrera 2009; Winter and Holtum 2014).

In contrast to  $C_3$  plants, CAM plants open their stomata at night, allowing net  $CO_2$  uptake from the atmosphere when the air temperature and vapor pressure deficit (vpd) are lower than during the day, during which the stomata of CAM plants are closed. This reversed stomatal activity, relative to non-CAM plants, reduces the amount of water lost per unit of carbon assimilated during 24-h periods, thus resulting in very high water-use efficiencies in CAM plants (Kluge and Ting 1978; Winter 1985; Lüttge 1987, 2004; Winter and Smith 1996; Herrera 2009). As a result, CAM species are typically widely distributed throughout arid and semi-arid regions of the world. But there are also some CAM plants in humid tropical and subtropical environments, these typically growing as epiphytes on trees. Epiphytes often lack soil or other water-holding media, such that their microenvironment can be quite arid, especially between rainfalls (Martin 2010).

Another adaptation to arid environments is water-storage tissue (succulence), and several studies of various taxa, including orchids, report good correlations between leaf succulence and the CAM photosynthetic pathway (Teeri et al. 1981; Winter et al. 1983; Griffiths et al. 2008; Martin et al. 2009). Although it has been argued that succulence of the photosynthetic tissue might impede  $CO_2$  uptake (Nelson et al. 2005;

Nelson and Sage 2008), Griffiths et al. (2008) provided evidence that the magnitude of CAM was positively associated with leaf succulence by investigating the interplay between carboxylase systems and light use in *Kalanchoe* species to counter this claim. Furthermore, Ogburn and Edwards (2010) illustrate that the increased degree of venation typically accompanying succulence provides additional benefits to such plants.

Many orchids, both  $C_3$  and CAM, possess a prominent, enlarged bulbous structure at the base of their leaves or extremely thickened stems, termed pseudobulbs (Hew and Yong 1997; Dressler 1981, 1993; Zimmerman 1990; Arditti 1992; Goh and Kluge 1989). Numerous authors claim that the primary function of the pseudobulb is water storage (Goh and Kluge 1989; Ertelt 1992; Hew and Yong 1997; He et al. 2011, 2013; Rodrigues et al. 2013; Yang et al. 2016), but they don't have enough experimental evidence to support this claim. Moreover, investigations that specifically focus on the putative water-storage role of pseudobulbs provide little convincing evidence of such role (Zheng et al. 1992; Stancato et al. 2001; He et al. 2013; Yang et al. 2016). Furthermore, evidence exists for other roles of the pseudobulb, including carbohydrate storage (Zimmerman 1990; Hew et al. 1998; Ng and Hew 2000; Stancato et al. 2001; Wang et al. 2008; He et al. 2011) and elemental nutrient storage (Zimmerman 1990; Ng and Hew 2000).

If pseudobulbs are important as water-storage organs, as often claimed (Goh and Kluge 1989; Hew and Yong 1997; Rodrigues et al. 2013; Yang et al. 2016), a logical deduction might be that such organs are more common and (or) larger in CAM orchids, relative to orchids with  $C_3$  photosynthesis, much as overall leaf succulence is correlated with CAM in orchids. On the other hand, because  $C_3$  orchids usually have thin, non-succulent leaves, it appears equally likely that these orchids might benefit from large water-storage organs, as pseudobulbs are claimed to be. In addition to these considerations, it is likely that habitat microenvironment also plays a role in the likelihood of any relationship between pseudobulb size and orchid photosynthetic pathway. For example, if CAM orchids are found in more xeric microenvironments than their  $C_3$  counterparts, it is reasonable to expect larger pseudobulbs in CAM orchids. Unfortunately, there are few studies of orchid microenvironments, especially those that distinguish  $C_3$  from CAM orchids in situ.

Therefore, the specific purpose of this study was to examine the relationship between pseudobulb size and photosynthetic pathway in over 100 species of  $C_3$  and CAM orchids growing in the greenhouses of the Missouri Botanical Garden, St. Louis, MO, USA. An overarching goal of this study was to gain further insight into the function of the orchid pseudobulb as a water-storage organ.

## Materials and Methods

### Plants

All the plants sampled (103 species) were growing in the greenhouses of the Missouri Botanical Garden, St. Louis, USA (38° 36'47" N; 90° 15'33" W). The sources and dates of plant acquisitions were not relevant to this study, but all plants were legally and ethically acquired using proper protocol and documentation. Ages of the plants were unknown, but most likely varied, as did length of time since acquisition in the greenhouse. All plants sampled appeared mature, and many were flowering at the time of this study (November 2017). Although sample sizes (*N*) for some species were up to 14, *N* was only one or two for few species. Typical environmental conditions, including on the day of measurements, in the greenhouses were natural sunlight (although filtered by the glasshouse roof and highly variable according to season and time of day, day/night air temperatures of approximately 20/13 °C, and day/night vapor pressure deficits of approximately 4.7/1.5 kPa. Watering and fertilization (20–10–10 NPK, plus micronutrients with Cu, Fe, Mn, Zn, B and Mo. COMPO EXPERT GmbH, Munster, Germany) regimes in the greenhouses varied by species, but all plants were well-watered when sampled for this study. Many of the plants were flowering

### Determination of pseudobulb volume

Pseudobulbs in this study were defined as distinct swellings or thickenings at the leaf bases or of the stems that subtended the majority of leaves on a stem. In the latter case, the stem-pseudobulbs were considerably thicker than the stems with many leaves attached (or with many leaf scars). In several cases, the pseudobulbs projected from leaf surfaces. In all species, considerable effort was expended to differentiate pseudobulbs from simple thick stems.

Pseudobulb size was determined from three measurements made on the pseudobulb of one leaf or stem for each plant (one or more plants per species) with a flexible, plastic cm rule. All measurements were made to the nearest mm. For all pseudobulbs that were either elongated (cylindrical or flattened) or spherical, the length was measured parallel to the stem; width was measured perpendicular to the stem; and thickness was also measured perpendicular to the stem, but at a 90° angle from the width measurement. To determine the volume of the pseudobulb, the equation for the volume of an ellipsoid ( $V_e$ ) or cylinder ( $V_c$ ) was employed

$$V_e = 4/3\pi lwt$$

$$V_c = \pi(0.5w)^2l$$

in which length (*l*), width (*w*), and thickness (*t*) represent the dimensions measured in the order described above.

When calculating  $V_c$ , *l* was 2 cm greater than the larger value of *w* or *t*, and *w* equals the average of *w* and *t*.

### Determination of photosynthetic pathway

The photosynthetic pathway ( $C_3$  or CAM; there are no known  $C_4$  orchids) for each species was determined by its leaf  $\delta^{13}C$  value or nocturnal increase in tissue titratable acidity reported in the literature (Avadhani et al. 1982; Earnshaw et al. 1987; Winter and Smith 1996; Hew and Yong 1997; Gehrig et al. 2001; Silvera et al. 2005, 2010b; Winter et al. 1983; Williams et al. 2001). Plants with  $\delta^{13}C$  less negative or equal to −20 ‰ were considered to be CAM, while those with values more negative than −20 ‰ were designated  $C_3$  plants. Any plant with a reported nocturnal increase in tissue acidity was also designated as a CAM plant, even though this definition also includes CAM-cycling plants. Plants lacking nighttime increases in acidity were considered to be  $C_3$  plants.

For each species in the study, the literature was examined for carbon isotopic or acidity data for species of the same name. Synonyms were used for some species. Failing such species epithet matches, one or more of the following approaches were used:

1. if at least 2/3 of the species in the same genus had the same pathway, it was assumed that all species in that genus shared that pathway.
2. if the above (1) applied to a genus that was very closely related to the genus of the species under consideration, its photosynthetic pathway was assumed to be that of the species in the other genus.
3. when all the above approaches failed, phylogenies of individual genera were consulted (Smidt et al. 2011; Wang et al. 2009; Williams et al. 2001; Winter and Smith 1996; Silvera et al. 2010a), and the photosynthetic pathway of the species under consideration was assumed to be the same as that of its most closely related sister species.

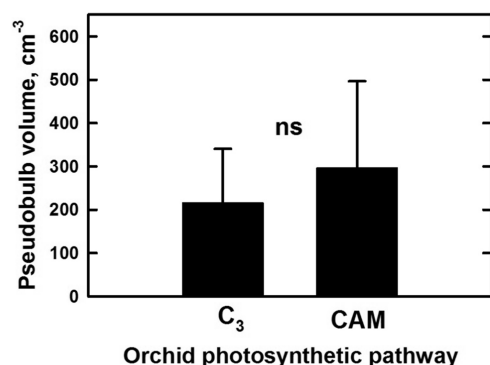
### Statistical analyses

Mean pseudobulb volumes for CAM and  $C_3$  species were compared with the Student *t*-test if the data met the assumptions for parametric statistics, or the Mann–Whitney *U*-test, when the data were heteroscedastic or not normally distributed (Sokal and Rohlf 2012). Significant differences were inferred when  $P \leq 0.05$ . All tests were performed by the SigmaPlot 12.5 (Systat Software, Inc., San Jose, CA) software package.

## Results

The sampled orchids comprised 57  $C_3$  species from 32 genera and 46 CAM species from 18 genera (Appendix A, Table A1) categorized in accordance with the approaches outlined in the Materials and Methods to determine the photosynthetic pathway. The number

**Fig. 1.** Mean (capped lines extending from bars = SE) pseudobulb volume of living orchids with the  $C_3$  photosynthetic pathway ( $N = 57$  species) or with CAM photosynthesis ( $N = 46$  species) growing in the greenhouses of the Missouri Botanical Garden. The means are not significantly different (ns;  $P > 0.05$ ).



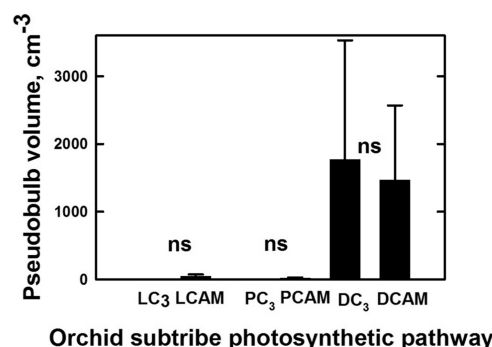
of taxa lacking pseudobulbs (21  $C_3$  and 23 CAM) was almost identical in the two photosynthetic pathway groups. The percentage of pseudobulb occurrence among  $C_3$  species was 63% and that among CAM species was 50%. The species lacking pseudobulbs were predominantly distributed in the genera *Dracula*, *Epidendrum*, *Dendrobium*, *Cattleya*, *Vanilla*, and *Phalaenopsis*. Although the pseudobulb volume of each species differed substantially (the largest pseudobulb volume was 8811.92 cm<sup>3</sup> and the smallest volume was 0 cm<sup>3</sup>), no significant difference between  $C_3$  and CAM orchid species was observed (Fig. 1).

To further explore the relationship between pseudobulb volume and photosynthetic pathway among orchids, the pseudobulb volumes of  $C_3$  and CAM species classified in three subtribes were compared (Fig. 2). Although the CAM species available for sampling far outnumbered the  $C_3$  species in the subtribes Laeliinae, Pleurothalliinae, and Dendrobiinae, pseudobulb volume was the same for  $C_3$  species and CAM species in all three subfamilies. The comparison of these three subtribes is clearly problematic as a result of the radical differences in the numbers of  $C_3$  and CAM species having pseudobulbs, but this problem was worse in comparisons of all other subtribes, as well as all tribes of taxa in the Orchidaceae (data not shown).

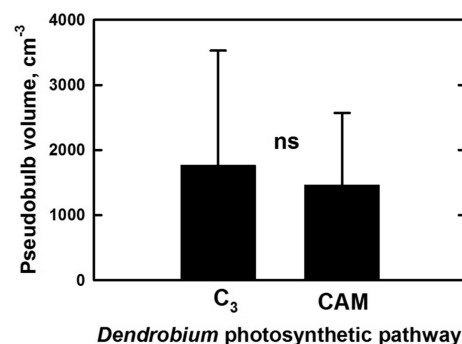
Finally, the pseudobulb volumes of eight CAM species of *Dendrobium* were identical to those of four  $C_3$  species of this genus (Fig. 3). No other sampled genus included a sufficient number of  $C_3$  and CAM species to allow a meaningful statistical comparison.

The results collectively indicated that there was no functional relationship between pseudobulb volume and photosynthetic pathway, or that the pseudobulb played an equally important role in  $C_3$  and CAM species in the Orchidaceae.

**Fig. 2.** Mean (capped lines extending from bars = SE) pseudobulb volume of living orchids with the  $C_3$  photosynthetic pathway [ $N = 4$  (L), 6 (P), 4 (D) species] or with CAM photosynthesis [ $N = 18$  (L), 4 (P), 8 (D) species] in each of three orchid subtribes [Laeliinae (L) and Pleurothalliinae (P), both in the tribe Calypsoeae, and Dendrobiinae (D) in the tribe Vandeeae] growing in the greenhouses of the Missouri Botanical Garden. The two photosynthetic pathway means for each subtribe are not significantly different (ns;  $P > 0.05$ ).



**Fig. 3.** Mean (capped lines extending from bars = SE) pseudobulb volume of living orchids in the genus *Dendrobium* with the  $C_3$  photosynthetic pathway ( $N = 4$  species) or with CAM photosynthesis ( $N = 8$  species) growing in the greenhouses of the Missouri Botanical Garden. The means are not significantly different (ns;  $P > 0.05$ ).



## Discussion

Overall, it is clear that pseudobulb volumes of  $C_3$  orchid species did not differ from those of the CAM species included in this study of over 100 species of living orchids in the greenhouses at the Missouri Botanical Garden. This was true when comparing all  $C_3$  and CAM species in the family, as well as comparing taxa with these two photosynthetic pathways in three subfamilies, and also in one genus. Therefore, the results of this study clearly indicate that pseudobulbs are equally important structures in both  $C_3$  and CAM orchid taxa. Previous work has indicated that orchid pseudobulbs are important for water, carbohydrate, and mineral storage (Goh and Kluge 1989; Zimmerman 1990; Ertelt 1992; Zheng et al. 1992; Yong and Hew 1995a; Hew and Yong 1997;



Hew et al. 1998; Wang et al. 2008; He et al. 2011; Rodrigues et al. 2013; Yang et al. 2016). The pseudobulb is an organ critical to the annual processes of growth, formation of new shoots, and flowering, and may also be crucial for the mobilization of reserves under abiotic stress (Hew et al. 1998; Stancato et al. 2001; Ng and Hew 2000). Pseudobulbs may mobilize water-soluble polysaccharides and release stored water to meet the transpirational demands of the leaves to slow the reduction in the leaf water content and decline in water potential, thereby enabling tolerance of relatively long periods of drought stress (Yang et al. 2016; He et al. 2013). Furthermore, a pseudobulb can use photosynthesis to contribute positively to the carbon balance by recycling respiratory carbon that would otherwise be lost (Arditti 1992; He et al. 2011, 2013). The present results suggest that all of these functions are apparently of equal importance in  $C_3$  and CAM orchids.

Many reviews of orchid structure and function claim that the primary function of pseudobulbs is water storage (Ertelt 1992; He et al. 2011, 2013; Rodrigues et al. 2013; Yang et al. 2016). Pseudobulbs can significantly increase the water storage capacity of a plant, thereby playing an essential role in helping species to survive prolonged periods of drought in epiphytic habitats, where water availability is often severely limited (Zotz and Tyree 1996; Zotz 1999). Pseudobulbs are able to retain approximately 64% of their water content after 42 d of water stress (Zheng et al. 1992). In some epiphytic orchid species, the pseudobulbs can survive for as long as 8 yr after the leaves abscise (Zotz 1998). If water storage is a primary function of the pseudobulb, which has currently not been definitively shown, this should be a particularly important adaptive feature of CAM orchids, which also rely on stored water in succulent leaves during rainless periods and which conserve water during nighttime stomatal opening in CAM. Such a morphological adaptation should also be of great importance for  $C_3$  orchids, which lack the high water-use efficiency of CAM taxa and, furthermore, have thin, non-succulent leaves. It is clear that the two groups of orchids, those with  $C_3$  photosynthesis and those with the CAM photosynthetic pathway, appear to be equally reliant on leaf/stem pseudobulbs for water, carbohydrates, and (or) essential elements. Further work is necessary to determine which of the latter three are of greatest importance to the two groups of orchid species. In addition, it would be valuable to know the actual water holding capacity of the different pseudobulbs, in addition to possible relationships between pseudobulb size and leaf area of the orchids.

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## Appendix A

**Table A1.** Pseudobulb volumes of 103 species of orchids.

Taxon	Tribe	Subtribe	Photosynthetic pathway	Pseudobulb volume (mean)/cm <sup>3</sup>
<i>Dracula erythrochaete</i>	Calypsoeae	Pleurothallidinae	C <sub>3</sub>	0
<i>Dracula cordobae</i>	Calypsoeae	Pleurothallidinae	C <sub>3</sub>	0
<i>Dracula mopsus</i>	Calypsoeae	Pleurothallidinae	C <sub>3</sub>	0
<i>Dracula bella</i>	Calypsoeae	Pleurothallidinae	C <sub>3</sub>	0
<i>Pleurothallis</i> sp.	Calypsoeae	Pleurothallidinae	C <sub>3</sub>	0
<i>Stelis argentata</i>	Calypsoeae	Pleurothallidinae	C <sub>3</sub>	0
<i>Arpophyllum giganteum</i>	Calypsoeae	Laeliinae	C <sub>3</sub>	0
<i>Epidendrum macroclinium</i>	Calypsoeae	Laeliinae	C <sub>3</sub>	0
<i>Epidendrum pseudepidendrum</i>	Calypsoeae	Laeliinae	C <sub>3</sub>	0
<i>Jacquinella equitantifolia</i>	Calypsoeae	Laeliinae	C <sub>3</sub>	0
<i>Brassia arcuigera</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	85.68
<i>Brassia caudata</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	38.27
<i>Brassia verrucosa</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	31.28
<i>Cuitlauzina egertonii</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	7.27
<i>Lockhartia micrantha</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	0
<i>Oncidium leucochilum</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	122.67
<i>Oncidium panamense</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	28.18
<i>Oncidium sphacelatum</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	102.12
<i>Trichopilia suavis</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	42.45
<i>Trichopilia turialbae</i>	Cymbidieae	Oncidiinae	C <sub>3</sub>	4.15
<i>Camaridium ochroleucum</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	340
<i>Christensonella uncata</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	0.18
<i>Heterotaxis discolor</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	151.46
<i>Heterotaxis valenzuelana</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	0
<i>Lycaste macrophylla</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	320.46
<i>Maxillaria endresii</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	45.02
<i>Maxillaria ringens</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	63.88
<i>Maxillaria</i> sp.	Cymbidieae	Maxillariinae	C <sub>3</sub>	10.22
<i>Maxillariella sanguinea</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	9.38
<i>Maxillariella tenuifolia</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	27.38
<i>Mormolyca ringens</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	185.31
<i>Trigonidium egertonianum</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	82.39
<i>Xylobium foveatum</i>	Cymbidieae	Maxillariinae	C <sub>3</sub>	54.81
<i>Gongora armeniaca</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	27.21
<i>Gongora quinquenervis</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	209.05
<i>Gongora unicolor</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	423.9
<i>Gongora pterodactyl</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	1009.61
<i>Gongora grosa</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	113.72
<i>Stanhopea cirrhata</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	157.79
<i>Stanhopea costaricensis</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	123.98
<i>Stanhopea</i> sp.	Cymbidieae	Stanhopeinae	C <sub>3</sub>	151.74
<i>Stanhopea wardii</i>	Cymbidieae	Stanhopeinae	C <sub>3</sub>	60.71
<i>Catasetum fimbriatum</i>	Cymbidieae	Catasetinae	C <sub>3</sub>	240.43
<i>Catasetum</i> sp.	Cymbidieae	Catasetinae	C <sub>3</sub>	448.49
<i>Spathoglottis plicata</i> var. <i>alba</i>	Vandaeae	Collabiinae	C <sub>3</sub>	23.4872
<i>Vanilla trigonocarpa</i>	Vanilleae	Epidendreae	C <sub>3</sub>	0
<i>Dendrobium gracilicaule</i>	Podochileae	Dendrobiinae	C <sub>3</sub>	0
<i>Dendrobium nobile</i>	Podochileae	Dendrobiinae	C <sub>3</sub>	0
<i>Dendrobium smilliae</i> ('Lea' × 'Aussie')	Podochileae	Dendrobiinae	C <sub>3</sub>	0
<i>Dendrobium chrysotoxum</i>	Podochileae	Dendrobiinae	C <sub>3</sub>	7059.3
<i>Paphiopedilum venustum</i> var. <i>album</i>	Cypripedeae	Paphiopediinae	C <sub>3</sub>	0
<i>Phragmipedium longifolium</i>	Phragmipediaceae	Phragmipediinae	C <sub>3</sub>	0
<i>Sobralia callosa</i>	Sobralieae	Sobraliinae	C <sub>3</sub>	0



Table A1. (concluded).

Taxon	Tribe	Subtribe	Photosynthetic pathway	Pseudobulb volume (mean)/cm <sup>3</sup>
<i>Vanda tessellata</i>	Vandaeae	Aeridinae	C <sub>3</sub>	0
<i>Bifrinaria harrisoniae</i>	Bifrinariaeae	Bifrinariinae	C <sub>3</sub>	0
<i>Phaius tankervilleae</i> 'Rabin's Raven'	Bifrinariaeae	Bletlinae Benth	C <sub>3</sub>	365.78
<i>Cirrhopetalum medusae</i>	Calypsoeae	Bulbophyllinae	C <sub>3</sub>	164.29
<i>Acianthera pubescens</i>	Calypsoeae	Pleurothallidinae	CAM	0
<i>Encyclia ceratistes</i>	Calypsoeae	Pleurothallidinae	CAM	12.87
<i>Encyclia cordigera</i> var. <i>alba</i>	Calypsoeae	Pleurothallidinae	CAM	52.7
<i>Encyclia pygmea</i>	Calypsoeae	Pleurothallidinae	CAM	10.12
<i>Barkeria lindleyana</i>	Calypsoeae	Laeliinae	CAM	0
<i>Brassavola nodosa</i>	Calypsoeae	Laeliinae	CAM	0
<i>Cattleya forbesii</i>	Calypsoeae	Laeliinae	CAM	0
<i>Cattleya intermedia</i>	Calypsoeae	Laeliinae	CAM	0
<i>Cattleya labiata</i> var. <i>alba</i> ( <i>C. labiata</i> var. <i>alba</i> 'Extra' × self)	Calypsoeae	Laeliinae	CAM	0
<i>Cattleya loddigesii</i>	Calypsoeae	Laeliinae	CAM	0
<i>Cattleya mossiae</i>	Calypsoeae	Laeliinae	CAM	36.84
<i>Cattleya trianae</i> var. <i>albescens</i>	Calypsoeae	Laeliinae	CAM	7.36
<i>Cattleya walkeriana</i>	Calypsoeae	Laeliinae	CAM	8.05
<i>Cattleya warneri</i>	Calypsoeae	Laeliinae	CAM	27.38
<i>Epidendrum ciliare</i>	Calypsoeae	Laeliinae	CAM	19.3
<i>Epidendrum ibaguense</i>	Calypsoeae	Laeliinae	CAM	0
<i>Epidendrum oerstedii</i>	Calypsoeae	Laeliinae	CAM	42.29
<i>Epidendrum peperomia</i>	Calypsoeae	Laeliinae	CAM	0
<i>Epidendrum schlechterianum</i>	Calypsoeae	Laeliinae	CAM	0
<i>Epidendrum stamfordianum</i>	Calypsoeae	Laeliinae	CAM	39.67
<i>Laelia rubescens</i>	Calypsoeae	Laeliinae	CAM	92.78
<i>Myrmecophila tibicinis</i>	Calypsoeae	Laeliinae	CAM	522.1
<i>Oncidium</i> sp.	Cymbidieae	Oncidiinae	CAM	100.48
<i>Rossioglossum ampliatus</i>	Cymbidieae	Oncidiinae	CAM	261.53
<i>Campylocentrum micranthum</i>	Vandaeae	Angraecinae	CAM	0
<i>Heterotaxis sessilis</i>	Cymbidieae	Maxillariinae	CAM	0
<i>Oeceoclades maculata</i> ( <i>O. maculata</i> × self)	Cymbidieae	Eulophiinae	CAM	1.85
<i>Oeceoclades spathulifera</i>	Cymbidieae	Eulophiinae	CAM	18.09
<i>Bulbophyllum baileyi</i>	Vandaeae	Dendrobiinae	CAM	16.75
<i>Bulbophyllum macranthum</i>	Vandaeae	Dendrobiinae	CAM	22.08
<i>Bulbophyllum macrobulbum</i>	Vandaeae	Dendrobiinae	CAM	646.11
<i>Bulbophyllum elassogossum</i>	Vandaeae	Dendrobiinae	CAM	5.43
<i>Vanilla planifolia</i>	Vanilleae	Epidendreae	CAM	0
<i>Vanilla pompona</i>	Vanilleae	Epidendreae	CAM	0
<i>Dendrobium bigibbum</i>	Dendrobieae	Dendrobiinae	CAM	30.74
<i>Dendrobium discolor</i>	Dendrobieae	Dendrobiinae	CAM	0
<i>Dendrobium lichenastrum</i>	Dendrobieae	Dendrobiinae	CAM	0
<i>Dendrobium speciosum</i> var. <i>hillii</i>	Dendrobieae	Dendrobiinae	CAM	2862.72
<i>Dendrobium teretifolium</i>	Dendrobieae	Dendrobiinae	CAM	0
<i>Dendrobium tetragonum</i>	Dendrobieae	Dendrobiinae	CAM	0
<i>Dendrobium wassellii</i>	Dendrobieae	Dendrobiinae	CAM	0
<i>Dendrobium hillii</i>	Dendrobieae	Dendrobiinae	CAM	8811.92
<i>Phalaenopsis amabilis</i>	Vandaeae	Aeridinae	CAM	0
<i>Phalaenopsis schilleriana</i>	Vandaeae	Aeridinae	CAM	0
<i>Phalaenopsis</i> sp.	Vandaeae	Aeridinae	CAM	0
<i>Angraecum sesquipedale</i>	Angraeeae	Angraecinae	CAM	0