

# Physiological roles of the green *pseudobulb* in tropical epiphytic orchids

## Abstract

The green *pseudobulbs* of epiphytic orchids function as storage organs for water, mineral and carbohydrates. They are responsible for the ultimate re-distribution of assimilated carbon from the leaves to other plant organs. Our research suggested that they play crucial roles in regulation of leaf photosynthesis, growth, flower initiation and survival of orchids. When epiphytic orchids are subjected to environmental stress such as water deficit, we have also found that the *pseudobulbs* play an important role in maintaining the water level of leaves and thus protecting epiphytic orchids against drought stress.

**Keywords:** epiphytic orchids, growth, photosynthesis, pseudobulbs, drought stress

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## Introduction

Epiphytic orchids are typically found in tropical environments. Evolution of epiphytes has been postulated to result in the formation of the green *pseudobulbs*,<sup>1,2</sup> which is characterized by the presence of very thick cuticle, absence of stomata and the abundance of water-storing cells.<sup>3</sup> These 'false bulbs' are known to function as storage organs for water, mineral and carbohydrates, playing crucial roles in the growth and survival of epiphytic orchids.<sup>4,5</sup> In addition, photosynthesis of green *pseudobulbs* can contribute positively to carbon balance by recycling respiratory carbon that would otherwise be lost.<sup>6</sup> Although the leaves are main sources that supply carbon for inflorescence development, the green *pseudobulbs* is responsible for the ultimate re-distribution of assimilated carbon from the leaves to other plant organs.<sup>7</sup> As such, the green *pseudobulbs* can be envisioned to play an active regulatory role in assimilate partitioning as well as a passive role as a storage organ. Furthermore, the green *pseudobulbs* may serve as a reserve for water, minerals and carbohydrates when epiphytic orchids are subjected to environmental stress such as water deficit.<sup>8</sup> The main objective of mini review was to discuss the roles of green *pseudobulbs* in growth and development of epiphytic orchids. Photosynthetic capacity of the green *pseudobulb* and its roles in regulating leaf photosynthesis and protecting epiphytic orchids against drought stress were also addressed.

## Roles of green *pseudobulbs* in growth and development

During new shoot and floral development, the developing new organs demand a large proportion of the newly fixed carbon for their growth.<sup>9</sup> The volume of the green *pseudobulbs* affects the rate of growth and final size of the new shoot were observed in epiphytic orchid hybrid of *Cattleya forbesii* Lindl. X *Laelia tenebrosa* Rolfe.<sup>10</sup> The volume of the green *pseudobulbs* was greatly reduced at certain stage of the young shoot development, suggesting that some storage compounds of the green *pseudobulbs* might have been transferred to developing shoot. The volume of the green *pseudobulbs* increased again at the later stage of the young shoot development. However, shading of the green *pseudobulbs* affected the translocation of the nutrients to the young shoots, indicating that this relationship is light dependent.<sup>10</sup>

The size and maturity of the green *pseudobulbs* were also critical for the orchid plants to attain the capacity of flowering.

For instances, flower initiation in *Miltoniopsis* was most rapid, uniform and complete when green *pseudobulbs* had reached their maturation stage.<sup>11</sup> Although green *pseudobulbs* do not show any gaseous exchange in light or in darkness, photosynthesis do take place in green *pseudobulbs* when exposed to light, which is involved primarily in the refixation of respiratory CO<sub>2</sub> produced by the underlying massive parenchymatous tissues.<sup>12</sup> This contributes to an increase amount of carbon assimilates and hence more food can be translocated to the developing inflorescence.<sup>12</sup> In the study with *Oncidium Goldiana*, the amount of <sup>14</sup>C assimilates contributed by the leaves on different shoots showed a decreasing trend with increasing distance from the inflorescence of the current shoot.<sup>6</sup> It is logical that the green *pseudobulbs* received and accumulated more <sup>14</sup>C during the short period (8hours) after <sup>14</sup>CO<sub>2</sub> feeding from the source leaves. It was also found that the green *pseudobulbs* of *Spathoglottis unguiculata* accumulated higher percentage of <sup>14</sup>C assimilate during the vegetative stage than during the flowering stage.<sup>6</sup> With the present of new organs such as inflorescences, more photo assimilates are channeled to the developing inflorescences than to other parts of the plants. Hence, there was a substantial interaction between the developing inflorescences emerging from the current back shoot and photo assimilates exported from the green *pseudobulbs*.

## Photosynthesis of the green *pseudobulb* and its role in regulating leaf photosynthesis

The partitioning of assimilates between sources and sinks results in phloem translocation. A source may be defined as an exporter of sugars to the phloem and a sink is an importer of sugar from the phloem. Sink organs utilize the imported assimilates for growth, maintenance and storage.<sup>13</sup> In our previous study, we investigated source-to-sink relationship between leaves and green flower petals of CAM orchid *Dendrobium* cv. Burana Jade. It was found that green flower petals function as sinks and depend on carbohydrates exported from leaves for their development and growth.<sup>14</sup> In their natural habitat, would the leaves and green *pseudobulbs* function efficiently as source if the photosynthetic capacity of either part is removed? How does the changing of source/sink ratio regulate the photosynthesis of leaves

or green *pseudobulbs*? That the accumulation of photo assimilate in leaves has a role in regulation of photosynthetic rate was hypothesized as early as 1868 by Bouddinhault.<sup>15</sup> In plants, changes in the photosynthetic source/sink balance are important in regulating leaf photosynthetic rate through effects on the leaf carbohydrate status.<sup>16–18</sup> In our study with  $C_3$  orchid *Oncidium* Golden Wish, it was found that light saturation for photosynthesis and maximum photosynthetic rates were significantly higher in leaves than in green *pseudobulbs*. The green *pseudobulbs* also had lower light utilization than that of leaves.

Our results also revealed that low levels of carbohydrate in leaves after reducing photosynthetic source/sink balance adversely affected the photosynthetic rate of leaves for  $C_3$  orchid *Oncidium* Golden Wish.<sup>19</sup> Due to their lower photosynthetic capacities, green *pseudobulbs* function mainly as sinks. As *pseudobulbs* store a large amount of carbohydrates, leaves could depend on *pseudobulbs* carbohydrates to regulate their photosynthesis when their source capacity was removed.<sup>19</sup> Some researchers failed to relate photosynthetic rate to source-sink relationships, suggesting that photosynthesis per se does not allow to arrive at specific conclusions on source or sink limitation.<sup>20,21</sup> However, the large *pseudobulbs* of *Oncidium* Golden Wish, constitutes almost two-third of the total biomass, which clearly plays an important role in regulation of leaf photosynthesis and thus, the carbon balance of the plant.<sup>19</sup> Furthermore, the green *pseudobulbs* had significantly higher concentration of insoluble sugar than that of leaves.<sup>19</sup> The *pseudobulbs* could switch from acting as a strong carbohydrate sink when leaves were actively photosynthesizing to become a strong source when leaves were subjected to unfavorable conditions such as long period of cloudy days and drought.

Although the amount of imported assimilates was lower and reasons for mature leaves acting as a sink was unclear, mature orchid leaves that imported assimilates from other non-foliar photosynthetic organs were reported by a number of researchers.<sup>13,22–24</sup> Functioning primarily as sinks but with additional source capacity, *pseudobulbs* points to the dynamism and plasticity in plant growth and development. For horticultural practice, it would be useful to further understand how environmental conditions would ultimately modulate the pattern of growth and development through their effects on source/sink relations between leaves and green *pseudobulbs*.

## The roles of the green pseudobulb in protecting epiphytic orchids against drought stress

Epiphytic orchids are directly or indirectly exposed to natural air currents and solar radiation and receive only intermittent rains.<sup>10,25,26</sup> Among the many abiotic factors involved in the survival of epiphytes, water availability is probably the most important environmental factor limiting growth and survival of epiphytes.<sup>27–29</sup> Thus, tolerance to water deficit is a decisive factor in their survival. Water stored in the *pseudobulbs* of the epiphytic orchids may facilitate a slow reduction in the leaf water content and decline in water potential during a period of drought for protecting those plants against the effects of water deficits.<sup>1,4,5,10</sup> Although large amounts of water and carbohydrates are stored in the *pseudobulbs*, many epiphytic orchids are sensitive to prolonged water deficit. It was reported that relative water content (RWC) decreased continuously in leaves and *pseudobulbs* of epiphytic CAM orchid (*Cattleya forbesii* Lindl × *Laelia tenebrosa* Rolfe) after they were subjected to drought stress up to 45 days.<sup>10</sup> Yang et al.<sup>30</sup> examined the anatomical traits, water loss rates, and physiology of leaves and *pseudobulbs* of four *Dendrobium* species with different

*pseudobulb* morphologies. Their results indicate that *Dendrobium* species with thin cuticles tend to have *pseudobulbs* with high water storage capacity that compensates for their faster rates of water loss. In our study, the decrease of water content in CAM orchid *Cattleya laeliocattleya* Aloha Case was much greater in *pseudobulbs* than in leaves after subjecting to drought stress, indicating that *pseudobulbs* facilitated a slow reduction in the water content of leaves. This finding was supported by the result of RWC of leaves, which started to decrease only after 3 weeks of drought stress. Our results also showed that decreases in total chlorophyll content, photosynthetic light use efficiency and CAM acidity were much less in leaves than in *pseudobulbs*.<sup>31</sup> Compared to leaves, although *pseudobulbs* were more sensitive to drought stress, to a certain extent *pseudobulbs* played an important role in maintaining the water level of leaves. Thus, the green *pseudobulbs* play an important role in protecting epiphytic orchids against drought stress.

## Conclusion

By understanding the physiological roles of green *pseudobulb* in tropical epiphytic orchids, it will be able to provide scientific basis for a large scale of gene expression analysis involved in the mechanisms responsible for water, mineral and carbohydrate storage and re-distribution. For horticultural practice, it would be useful to understand how environmental conditions would ultimately modulate the pattern of growth and development through its effects on source/sink relations between green leaves and green *pseudobulb*. Therefore, more attention would be pay to the growth management of the *pseudobulb*. By evaluating the physiological role of the pseudobulb in response to drought stress, a better understanding how abiotic factors are limiting epiphyte growth and survival which, in turn, should affect epiphyte community composition.

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## Conflict of interest

The author declares there is no conflict of interest regarding the publication of this article.

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