Review

Orchid pseudobulbs – ‘false’ bulbs with a genuine importance in orchid growth and survival!

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Abstract

Most orchids have conspicuous storage organs. For epiphytic orchids, storage organs are enlarged stems called pseudobulbs. Considerable efforts have been devoted to the study of orchids in recent years. In contrast, few studies have examined the role of pseudobulbs in orchid growth and survival. This paper reviews the photosynthetic role of pseudobulbs, its role in partitioning of assimilates and storage of water, carbohydrate and minerals. Results from the handful of studies of orchid pseudobulbs have shown these specialised structures to be of central importance in the growth and survival of orchids. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The family Orchidaceae is one of the largest and most diverse families of flowering plants. Orchids are either terrestrial or epiphytic in nature. Although a cosmopolitan family, epiphytic orchids are limited to tropical and sub-tropical environments (Dressler, 1981). Most orchids have conspicuous storage organs. Corms, rhizomes, or tuberoids are common in terrestrial orchids while storage organs in epiphytic orchids are enlarged stems called pseudobulbs (Dressler, 1981; Zimmerman, 1990; Arditti, 1992). Pseudobulbs are also present in some terrestrial orchids like Cymbidium, Eulophia and Spathoglottis.

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Orchid pseudobulbs can be of two types: heteroblastic or homoblastic. Heteroblastic pseudobulbs are composed of only one internode, e.g. *Oncidium*, *Cattleya* and *Miltonia*. Homoblastic pseudobulbs consist of two or more internodes of varying or similar lengths, e.g. *Eria* and *Dendrobium*. The homoblastic pseudobulb is generally considered to be the more primitive of the two (Dressler, 1981).

Much effort have been devoted to the study of orchids, e.g. mineral nutrition (Poole and Sheehan, 1980; Hew and Ng, 1996), respiration (Hew, 1987), photosynthesis (Neales and Hew, 1975; Hew, 1976; Avadhani et al., 1982; Hew et al., 1984, 1989, 1996, 1997; Hew and Yong, 1994; Ng and Hew, 1999), flowering (Goh et al., 1982), flower physiology (Avadhani et al., 1994) and more recently, photoassimilate partitioning (Clifford et al., 1992; Wadasinghe and Hew, 1995; Yong and Hew, 1995a, b, c; Ng and Hew, 1996). In these approaches, few studies have been devoted to the role of pseudobulbs in orchid growth and survival. Nevertheless, results from the handful of studies on orchid pseudobulbs have shown these specialised structures to be of central importance in the growth and survival of orchids.

2. Pseudobulbs as water storage organs

Orchid pseudobulbs are important water storage organs. The epiphytic biotope is characterised by frequent periods of water and nutrient shortage. Presence of fleshy organs in roots, stems or leaves confers epiphytic orchids the ability to survive and grow in these harsh environments. Pseudobulbs of *Oncidium* Goldiana maintain relatively high water contents of 90–95% throughout development (Hew and Ng, 1996). Studies on *Stanhopea* and *Pleione* have shown that pseudobulbs are made up of an abundance of water-storing cells (Chiang and Chen, 1968; Stern and Morris, 1992). In addition, most orchid pseudobulbs possess a thick cuticle and are totally impervious to water and gases (Arditti, 1992).

The importance of the pseudobulb in whole plant water economy was further substantiated in experiments with the terrestrial orchid, *Cymbidium sinense*. In this study, it was demonstrated that pseudobulbs were able to retain about 64% of their water content after 42 days of water stress conditions (Zheng et al., 1992). It is conceivable, therefore, that the evolution of epiphytes and the conquest of dry habitats should lead to the development of pseudobulbs.

3. Pseudobulbs as mineral storage organs

Epiphytic orchids encounter frequent periods of nutrient scarcity. They are tolerant of low substrate fertility, being totally dependent on stem flow for nutrient. The low fertility tolerance of orchids is closely associated with the
development of the pseudobulb. Tissue analyses of *Laeliocattleya* Culminant have shown that there was net accumulation of nitrogen and phosphorus with age. In contrast, potassium content decreased with age, suggesting that potassium was possibly remobilised to support the growth requirements of new developing tissues (Davidson, 1960).

In *Oncidium* Goldiana, it was observed that uptake of nitrate was highest during the formation of new pseudobulbs (Hew, unpublished). In addition, it was observed that mineral allocation to pseudobulbs within connected shoots of *Oncidium* Goldiana was most active during formation and development of a new pseudobulb (Hew and Ng, 1996). There were observable reductions in the mineral content of mature pseudobulbs of connected shoots during the development of a new shoot (Hew and Ng, 1996). The remobilisation of stored mineral nutrients from older pseudobulbs coupled with the high rates of nutrient uptake is indicative of the demand for mineral nutrients by developing pseudobulbs. As such, it is important to leave connected back shoots intact during the propagation of sympodial orchids. The active accumulation of mineral nutrients during the period of pseudobulb development constitutes an important source of reserve for the subsequent development of the inflorescence and new shoots (Hew and Ng, 1996). Storage minerals of *Catasetum viridiflavum* have also been shown to be important in determining the number of flowers produced (Zimmerman, 1990). It is therefore recommended that special attention be paid to the fertilisation regime, especially during the period of new shoot development.

### 4. Pseudobulb photosynthesis

Photosynthesis is the process whereby carbon dioxide from the atmosphere is fixed into sugars in green plant organs. Leaves are the main photosynthetic organs in most plants. In addition to leaves, several other non-foliar organs of orchids possess chlorophyll and are capable of fixing carbon dioxide. Benzing and Pockman (1989) have shown that fruit capsules of *Encyclia tampensis* are capable of limited amounts of gas exchange with the environment and suggested that non-foliar green organs of orchids do contribute positively to whole plant carbon economy by refixing the carbon which would otherwise be lost through respiration. The same cannot be said about pseudobulbs. Most orchid pseudobulbs are impervious to water and gases due to the presence of a thick cuticle. The pseudobulb, a massive organ, therefore represents a substantial cost in terms of carbon for maintenance.

Although impervious to water and gases, pseudobulbs of *Oncidium* Goldiana, nevertheless are capable of photosynthesis. Pseudobulb photosynthesis in *Oncidium* functions essentially for the refixation of respiratory carbon produced by the underlying massive parenchyma (Hew and Yong, 1994). Enzymes for
carbon fixation (ribulose-1,5-bisphosphate carboxylase/oxygenase and phosphoenolpyruvate carboxylase) are present within the tissue of the pseudobulb (Hew et al., 1996). While most orchids are impervious to the external environment, gas exchange with the ambient atmosphere is mediated by a cavity rich in stomata on top of the pseudobulb in *Bulbophyllum minustissimum*. This is especially important, as the leaves of this orchid are rudimentary (Winter et al., 1983).

In the CAM orchid, *Laelia anceps*, photosynthesis of leaves was largely influenced by irradiance of the pseudobulb (Ando and Ogawa, 1987). Exposure of the pseudobulb to light was necessary for leaves to conduct daily gas exchange with the atmosphere. It has been proposed that the organic acid fixed during the night is transported to the pseudobulb and decarboxylated the next day and that the transport of organic acid is enhanced by exposure of the pseudobulb to light. It appears that the pseudobulb can regulate the capacity for CAM in leaves of *Laelia anceps* although evidence in CAM orchids for the basipetal transport of organic acids from leaves to pseudobulb is lacking. Presently, it is unknown whether pseudobulbs of C₃ and CAM orchids have a regulatory role in leaf photosynthesis. However, growers, when considering lighting regimes for their orchid plants should take into account light requirements of both leaves and pseudobulbs. In addition, the correct definition of optimal light regimes has a direct implication on the planting density of orchids. Excessive shading must be avoided.

5. Pseudobulbs as carbohydrate storage organs

The ability of orchid pseudobulbs to photosynthesise points to the importance of the pseudobulb as a carbon source for the plant. Studies on both *Catasetum viridiflavum* (Zimmerman, 1990) and *Oncidium Goldiana* (Hew and Ng, 1996) have shown that carbohydrate reserves in orchid pseudobulbs are important in the initiation of new growth. The pseudobulb of *Oncidium* accumulates massive amounts of carbohydrates during vegetative development. These carbohydrate reserves are subsequently remobilised to support new shoot and inflorescence development (Hew and Ng, 1996).

Storage carbohydrate of the pseudobulb is derived mainly from the import of currently assimilated carbon from the leaves (Yong and Hew, 1995a) and in part from its own regenerative photosynthesis (Hew and Yong, 1994; Yong and Hew, 1995b; Hew et al., 1996). The carbohydrate reserves of connected back shoots also contribute to new shoot and inflorescence development (Yong and Hew, 1995c, Hew and Ng, 1996). While leaves are the main sources of currently assimilated carbon, pseudobulbs represent an important supplementary source of carbohydrate that is utilised to meet the increased demand for carbon during inflorescence and new shoot development. This observation is important and
explains the need for at least two connected back shoots for optimal inflorescence development (Yong and Hew, 1995b, c).

6. The absence of a ‘flag’ leaf – an apparent anomaly due to the pseudobulb

A ‘flag’ leaf is defined as the main leaf responsible for supplying carbon to the organ of economic importance. This is usually the leaf subtending the economically important organ. A typical example is seen in cereals such as wheat. The developing ear derived carbon mainly from the subtending ‘flag’ leaf. Based on gas exchange studies on Oncidium Goldiana, Hew and Yong (1994) showed that the rate of carbon dioxide uptake for the leaf subtending the inflorescence increased 1.4 fold during inflorescence development while the rate of carbon dioxide uptake for other mature leaves remained unchanged. This indicated that the leaf subtending the inflorescence is the ‘flag’ leaf. However, radioactive carbon tracer studies showed an absence of a ‘flag’ leaf in Oncidium Goldiana. All mature leaves within a single shoot supplied similar amounts of carbon to the inflorescence (Yong and Hew, 1995a, 1996). On the basis of radioactive tracer studies, Yong and Hew (1995a) concluded that there is an absence of a ‘flag’ leaf in Oncidium Goldiana. This apparent anomaly between gas exchange studies (Hew and Yong, 1994) and radioactive tracer studies (Yong and Hew, 1995a) is interesting.

Radioactive tracer studies showed that carbon produced in the leaves is transported to the pseudobulb in the first instance (Yong and Hew, 1995a) before being transported to the inflorescence. Tissue analyses of pseudobulb carbohydrate content showed that there was no net accumulation of carbohydrate during inflorescence development (Hew and Ng, 1996). Taken together, these results indicated that there is substantial mobilisation of carbohydrate to the inflorescence via the pseudobulb. It is likely that there is mixing of different carbohydrate pools (currently assimilated carbon from leaves with storage carbohydrate within the pseudobulb) during the transport of carbon from leaves to the inflorescence. The pseudobulb can be envisaged as central to the distribution of carbon within a single shoot of Oncidium Goldiana. Although the leaves are main sources that supply carbon for inflorescence development, the pseudobulb is responsible for the ultimate re-distribution of assimilated carbon from the leaves. This could account for the apparent absence of a ‘flag’ leaf in Oncidium based on radioactive tracer studies. Further work needs to be done to substantiate the possible regulatory role of pseudobulbs in partitioning of assimilates in orchids.

7. Pseudobulbs and myrmecophily

Ants, the most common arboreal insects of tropical rainforests are in frequent contact with epiphytic plants. The existence of ant-epiphytic interactions in
orchids is therefore not unusual. Association between ants and orchids can be broadly classified into two categories: (1) ant-house and (2) ant-garden (Davidson and Epstein, 1989). Ant-house orchids are characterised by the presence of a permanent dormatia in which ants take up residence while ant-gardens are nests of earthen material (called ‘carton’) constructed by ants on which the epiphyte grows (Beattie, 1985; Kleinfeldt, 1986). Species that have been classified as ant-house orchids include Caulathron, Dimeranda and Schomburgkia while Vanilla planifolia has been reported to be an ant-garden orchid (Davidson and Epstein, 1989). There is evidence to suggest that in both ant-house and ant-garden epiphytes, the ant-epiphyte association is mutualistic (Davidson and Epstein, 1989). In the CAM orchid Schomburgkia humboldtiana, leaves grow from a large pseudobulb that is hollow and contains ant-nests (Griffiths et al., 1989). Little is known about the precise ant-epiphytic relationship in Schomburgkia and other orchids. However, it appears that the hollow pseudobulb of Schomburgkia humboldtiana forms spontaneously without excavation by ants (Griffiths et al., 1989). This appears likely to be the result of coevolution although the actual relationship remains to be unequivocally determined.

The occurrence of an ant-house in pseudobulbs of Schomburgkia provides an interesting material for investigating the physiological role of the pseudobulb. It is likely that the physiological role of the hollow pseudobulb of Schomburgkia is different from those of other orchids like Dendrobium, Cattleya, Oncidium and Laelia. While pseudobulbs of Oncidium, Cattleya and Dendrobium are likely to participate in a myriad of physiological processes, the same cannot be affirmed for pseudobulbs of Schomburgkia with certainty. It is unlikely that pseudobulbs of Schomburgkia are important in water storage. However, it is possible for the pseudobulb of Schomburgkia to contribute to whole plant mineral and carbon economy through its association with ants. It is possible that the provision of an ant-house in the hollow pseudobulb constitutes an additional food source in the form of ant faeces and refuse. In addition, the fixation of respiratory carbon from ants may have a positive contribution to whole plant carbon economy.

8. Conclusion

Orchid pseudobulbs are engaged in a myriad of physiological processes that are important for growth and survival. The ability to store water, mineral and carbohydrates in the pseudobulb has serious implications for survival in the harsh and nutrient limited epiphytic biotope. Pseudobulb photosynthesis recycles respiratory carbon that would otherwise be lost, thus, contributing positively to whole plant carbon economy. In addition, the pseudobulb is central in the distribution of carbon within the plant. More studies of both C₃ and CAM orchids with diverse structural and morphological characteristics will undoubtedly
advance our understanding of the contribution of pseudobulbs to whole plant physiology of this fascinating group of plants.

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References


