Research Paper

Volume : 3 | Issue : 12 | December 2014 • ISSN No 2277 - 8179

Physiology of Temperate and Tropical Orchids-An Overview

Agriculture

KEYWORDS : Orchids, epiphytic, terrestrial, pseudobulbs, C3, C4, CAM, photosynthesis

N. Sailo	NRC for Orchids, Pakyong, Sikkim
Deepak Rai	NRC for Orchids, Pakyong, Sikkim
L.C. De	NRC for Orchids, Pakyong, Sikkim

ABSTRACT

Epiphytic orchids are characterized by thick and succulent leaves with thick cell walls, cuticles and small substomatal chamber whereas those of terrestrial species are thin. Usually mature leaves are photosynthetically active. The base of the stem of sympodial epiphytes, or in some species essentially the entire stem, may be thickened to form what is called a pseudobulb that contains nutrients and water for drier periods. Terrestrial orchids may be rhizomatous or form corms or tubers which contain reserve carbohydrates. A marked increase in respiration following pollination has been observed in orchids. Activities of a number of enzymes like catalase, peroxidase, polyphenol oxidase, ascorbic acid oxidase and glycolic acid oxidase increased following pollination. All orchid species are mycoheterotrophic during germination and reliant upon fungi to complete their lifecycle. All thin leaved orchids fix CO2 via C3 pathway. C4 pathway occurs primarily in plants of tropical origin growing under high light and high temperature conditions, E.g, Arundina graminifolia. The majority of plants in the Orchid family uses Crassulacean Acid Metabolism or CAM photosynthesis to fixate carbon dioxide. In these plants, the carboxylating enzyme for dark fixation is phosphoenolpyruvate carboxylase (PEPCase). An orchid leaf will have greater rates of photosynthesis at higher levels of atmospheric CO2 concentration. In Cymbidium, the process from flower bud induction in the new growth to blooming can be divided into three stages, Flower Bud Initiation in the New Growth (Stage I), Flower Spike Initiation (Stage II) and Spike Elongation and Blooming (Stage III). Orchid pseudobulbs serve as water storage, carbohydrate storage and mineral storage organ.

Introduction

Orchids are bilaterally symmetric (zygomorphic), many resupinate, one petal (labellum) is always highly modified, stamens and carpels are fused, and the seeds are extremely small.

Leaves: Like most monocots, orchids generally have simple leaves with parallel veins, although some Vanilloideae have a reticulate venation. They may be ovate, lanceolate, or orbiculate and very variable in size. They are normally alternate on the stem, often plicate, and have no stipules. Orchid leaves often have siliceous bodies called stegmata in the vascular bundle sheaths (not present in the Orchidoideae) and are fibrous.

The attractive mottle of the leaves of Lady's Slippers from tropical and subtropical Asia, (*Paphiopedilum*) is caused by uneven distribution of chlorophyll. Also *Phalaenopsis schilleriana* is a pastel pink orchid with leaves spotted dark green and light green. The Jewel Orchid (*Ludisia discolor*) is grown more for its colorful leaves than its fairly inconspicuous white flowers. Number of stomata per unit surface area is always higher in upper leaves on the same stem due to stronger light intensity on the upper leaves. Epiphytes generally have smaller stomata than terrestrial species. Epiphytic orchids are characterized by thick and succulent leaves with thick cell walls, cuticles and small substomatal chamber whereas those of terrestrial species are thin. Usually mature leaves are photosynthetically active. Leaves are sites for reduction of transpiration, water storage organs, retention of rain or condensed water and absorption of water as liquid or vapour.

The hard leathery leaf type of orchids are drought tolerant with very thick cuticle and thick walled epidermis together with extensive lignification offer excellent protection against desiccation. Thick leaves have Crassulacean Acid Metabolism (CAM), a very important adaptation to water stress. All thin orchid leaves show C_3 photosynthesis. Small and narrow leaves are better adapted exposed sites than larger ones because they lose heat more efficiently by convection. Leaf hair may help conserve water by increasing the boundary layer thickness of air around the leaf and lengthening the diffusion pathway. Deciduousness occurring in sympodial orchids avoid water stress during the dry season by shedding their leaves and entering a dormancy period. Water may be stored in pseudobulbs or other parts of the plant.

Stem and roots: All orchids are perennial herbs and grow according to two patterns.

Monopodial: The stems grows from a single bud, leaves are added from the apex each year and the stem grows longer accordingly e.g., Vanda and Vanilla.

Sympodial: The plant produces a series of adjacent shoots which grow to a certain size, bloom and then stop growing, to be then replaced. The base of the stem of sympodial epiphytes, or in some species essentially the entire stem, may be thickened to form what is called a pseudobulb that contains nutrients and water for drier periods, e.g., Cymbidium, Cattleya.

Terrestrial orchids: Terrestrial orchids may be rhizomatous or form corms or tubers which contain reserve carbohydrates. Glucomannan is the major constituent of reserve carbohydrate in tubers. The free mannose, glucose, manobiose and maltose formed from the reserve polysaccharides are transformed to sucrose and transported to new tubers and to the newly formed upper part of plant. In warm and humid climates, many terrestrial orchids do not need pseudobulbs. Epiphytic orchids have modified aerial roots that are sometimes be a few meters long. In the older parts of the roots, a modified spongy epidermis called velamen has the function to absorb humidity. It is made of dead cells and can have a silvery-grey, white or brown appearance. The cells of the root epidermis grow at a right angle to the axis of the root to allow them to get a firm grasp on their support. Nutrients mainly come from animal droppings and other organic detritus on their supporting surface.

Flower: Orchidaceae are popular for their structural variations in their flowers. Some orchids have single flowers but most have a racemose inflorescence, sometimes with a large number of flowers. The flowering stem can be basal, that is produced from the base of the tuber, like in Cymbidium, apical, meaning it grows from the apex of the main stem, like in Cattleya, or axillary, from the leaf axil, as in Vanda. The orchid flower, like most flowers of monocots has two whorls of sterile elements. The outer whorl has three sepals and the inner whorl has three petals. The sepals are usually very similar to the petals but may be completely distinct. The upper medial petal, called the labellum or lip is always modified and enlarged. The inferior ovary or the pedicel usually rotates 180 degrees, so that the labellum, goes on the lower part of the flower, thus becoming suitable to form a platform for pollinators. This characteristic, called resupination occurs primitively in the family and is considered apomorphic. Some orchids have secondarily lost this resupination, e.g. *Zygopetalum* and *Epidendrum secundum.*

A pollinium is a waxy mass of pollen grains held together by the glue-like alkaloid viscin, containing both cellulosic stands and mucopolysaccharides. Each pollinium is connected to a filament which can take the form of a caudicle, like in Dactylorhiza or Habenaria or a stipe, like in Vanda. Caudicles or stipes hold the pollinia to the viscidium, a sticky pad which sticks the pollinia to the body of pollinators. At the upper edge of the stigma of single-anthered orchids, in front of the anther cap, there is the rostellum, a slender extension involved in the complex pollination mechanism. In Cattleya cut flowers, the respiration rate decreases with age. Tight buds had the highest rates of respiration which declined after the opening of bud. All the young flowers respire at higher rates than the older ones.

Pollination: Orchids have developed highly specialized pollination systems. Orchid flowers usually remain receptive for very long periods and most orchids deliver pollen in a single mass; each time pollination succeeds thousands of ovules can be fertilized.

Pollinators are often visually attracted by the shape and colours of the labellum. Some orchids mainly or totally rely on self-pollination, especially in colder regions where pollinators are particularly rare. The caudicles may dry up if the flower hasn't been visited by any pollinator and the pollinia then fall directly on the stigma. Otherwise the anther may rotate and then enter the stigma cavity of the flower (as in *Holcoglossum amesianum*). In some extremely specialized orchids, like the Eurasian genus *Ophrys*, the labellum is adapted to have a colour, shape and odour which attracts male insects via mimicry of a receptive female. Pollination happens as the insect attempts to mate with flowers. Many neotropical orchids are pollinated by male orchid bees, which visit the flowers to gather volatile chemicals they require to synthesize pheromonal attractants. Each type of orchid places the pollinia on a different body part of a different species of bee, so as to enforce proper cross-pollination.

A marked increase in respiration following pollination has been observed in orchids. Activities of a number of enzymes like catalase, peroxidase, polyphenol oxidase, ascorbic acid oxidase and glycolic acid oxidase increased following pollination. Activity of polyphenol oxidase in orchids is reported highest in the columns followed by aerial roots, tips, petals and leaves. A dramatic increase in catalase activity is observed in columns and petals of *Cymbidium lowianum* and *Dendrobium nobile* after pollination. The sharp rise in peroxidase activity in aging orchid flowers is caused by an increase in ethylene production during senescence.

Fruits and Seeds: The ovary typically develops into a capsule that is dehiscent by 3 or 6 longitudinal slits, while remaining closed at both ends. The ripening of a capsule can take 2 to 18 months. The seeds are generally almost microscopic and very numerous, in some species over a million per capsule. After ripening they blow off like dust particles or spores. They lack endosperm and must enter symbiotic relationship with various mycorrhizal basidiomyceteous fungi that provide them the necessary nutrients to germinate, so that all orchid species are mycoheterotrophic during germination and reliant upon fungi to complete their lifecycle.

Photosynthesis

C_3 –Photosynthesis: All thin leaved orchids fix CO_2 via C_3 pathway. The thin leaved orchids have fewer layers of smaller mesophyll cells and a larger number of stomata than thick leaved species. They have high CO_2 points, prominent post-illumination CO_2 outbursts and active glycolic acid activity all of which are characteristics of plants with high photorespiration.E.g., *Habenaria platyphylla, Arundina graminifolia, Coelogyne masangeana, Cymbidium cynense, Oncidium spp, Vanda tessellata, Eulophia keithii, Spathoglottis plicata.*

C_4-Photosynthesis: PEP is the initial C-acceptor and the product is oxaloacetate which is readily converted to malate or aspartate. The malate is then decarboxylated to yield CO_2 which is refixed by RUBP carboxylase. C4 pathway occurs primarily in plants of tropical origin growing under high light and high temperature conditions. E.g, *Arundina graminifolia.*

Crassulacean Acid Metabolism (CAM): The majority of plants in the Orchid family uses Crassulacean Acid Metabolism or CAM photosynthesis to fixate carbon dioxide. In these plants, the carboxylating enzyme for dark fixation is phosphoenolpyruvate carboxylase (PEPCase). PEPCase has a high affinity for the CO2 molecule. Plants open their stomata during the cooler and more humid night-time hours, permitting the uptake of carbon dioxide with the minimum water loss. During the day, they close their stomata and concentrates CO_2 around the enzyme RuBisCO increasing its efficiency. E.g., *Vanilla, Cattleya, Thunia marshiliana, Coelogyne cristata, Laelia spp, Dendrobium, Calanthe vestita, Bulbophyllum, Aerides odoratum, Phalaenopsis, Aranda, Aranthera.*

CO_2 Enrichment and Orchid growth

CO_2 enrichment generally causes plants to develop more extensive root systems to exploit additional pockets of water and nutrients and to enhance the activity of bacteria and other organisms that break nutrients out of the soil, which the plants can then exploit.

It is generally accepted that orchids have either C_3 or Crassulacean Acid Metabolism (CAM) mode of photosynthesis, and these are usually associated with thin or thick leaves (Hew and Yong, 1997). In C_3 photosynthesis, the carboxylating enzyme Rubisco has a relatively low affinity for CO_2 molecule and therefore an increase in CO_2 concentration will increase the rate of CO_2 fixation. An increase in CO2 concentration will also inhibit the rate of photorespiration. The net effect of these two events is an increase in net photosynthesis (Drake *et al.*, 1997).

An orchid leaf will have greater rates of photosynthesis at higher levels of atmospheric CO_2 concentration. This in turn will generate more carbohydrate available for growth and development.

Practical Aspects of CO_2 Enrichment: Carbon dioxide is generally introduced by one of three ways:

- Burning a hydrocarbon such as propane or kerosene.
- Placing containers of dry ice in the greenhouse or growth cabinet/room.
- Using pure carbon dioxide from a pressurized container.

The third option is the preferred one because pure CO_2 contains fewer growth limiting pollutants. For C_3 orchids (thin-leaved orchids like *Oncidium* 'Goldiana', *Spathoglottis plicata*), CO_2 enrichment should commence at sunrise or when photoperiod begins and refrain during darkness hours. The average CO_2 level that is recommended is 700 to 1500 ppm. For CAM orchids (thick-leaved orchids, like *Dendrobium* and *Phalaenopsis*), CO_2 enrichment should commence at three to four hours before sunset, continue through darkness hours and stop when photoperiod begins.

Growth Physiology stages in Cymbidium orchids

The process from flower bud induction in the new growth to blooming can be divided into three stages.

Stage I : Flower Bud Initiation in the New Growth
Stage II : Flower Spike Initiation
Stage III : Spike Elongation and Blooming

Stage I: Flower bud initiation in the new growth

This stage does not require the temperature as low as Stage II and III. Normally, flowering of a cymbidium is initiated within the new growing pseudobulb. Under suitable growing conditions, where night temperatures are below the plant's required maximum night temperature, their pseudobulbs will be bigger and healthier with larger and thicker leaves. Commonly, lower temperature at night reduces plant respiration; therefore plants deplete less stored energy. As a result, more energy is accumulated in their storage organs. Eventually, those pseudobulbs have a higher potential to produce better quality flowers with a higher flower count. If the required night temperatures are not fulfilled, pseudobulbs will tend to produce poorer quality flowers and a lower flower count per stem. In severe cases, they may not produce any blooms at all. It is a general rule that the large-flowered types need greater energy storage in their pseudobulbs than the smaller-flowered types do. In other words, the large-flowered types require lower night temperatures than the smaller-flowered types do. Traditionally, all the commercial large-flowered cymbidiums have been developed from large-flowered species that originated from the foothills of Himalayan Mountains, starting from northern India, Nepal, Bhutan, northern Burma, and southwestern China and throughout many smaller ranges in Vietnam, Laos and northern Thailand. In these original habitats, their climate is divided into wet and dry cycles.

- The wet season is the monsoon season of Asia. During this season, these areas receive ample rains with higher daytime temperatures. However, their nighttime temperatures drop drastically by 10 to 15°C and become cool. This is a common climatic occurrence at higher elevations. The monsoon season is also the season of active vegetative growth.

- The dry season is affected by the cold air-mass from northern Asia. Temperatures and humidity fall down. The monsoon rains completely stop. This is the time when the large-flowered cymbidium species stop vegetative growth , instead they enter into a reproductive cycle i.e. the season of blooming.

The Mediterranean climate zones, *cool summer /mild winter*, such as the southwestern coast of the US, southern coast of Europe and South Africa, southern and southwestern Australia and New Zealand are considered ideal for most of the commercial large-flowered hybrids, which came from the Himalayan species. Because of their relatively temperate summers, the summer nighttime temperatures drop markedly. And, there is rarely a freezing period prolonged enough to damage plants or developing flowers. All traditional cymbidium hybrids perform well happy under these conditions.

For areas of humid subtropical climates, with *hot summer and cool-cold winter*, such as most of the eastern coasts of various continents between latitude 25-40; e.g. southeastern & southern USA, southern & eastern China, most of Japan, the eastern coast of Australia, southeastern Brazil to northern Argentina, northern India and northern Vietnam, there is often a prolonged period of hot & humid summer weather, with high night temperatures. These conditions cause stress to conventional cymbidiums, and result in a lower energy storage in their pseudobulbs.

Such stress has a directly negative effect on the new pseudobulb growth during the summer. Those affected pseudobulbs may end up smaller than their genetic potential. As a result, those stunted pseudobulbs will produce inferior quality flowers and usually fewer spikes. In the worst scenario, those sub-standard pseudobulbs may not produce any blooms at all.

Nowadays, growers can overcome these kinds of problem by growing varieties with a mixed background of tropical lowland species, namely Heat Tolerant Cymbidiums (HTC) and Warmth Tolerant Cymbidiums (WTC). Both HTC and WTC do not require night temperatures as low as that of conventional or standard cymbidiums. In climates with a prolonged hot summer, the new growths of HTC and WTC will still initiate flower buds in their growths. Therefore, non-flowering or reduced-flowering growths can be overcome.

Stage II: Flower spike initiation

This stage requires maximum night temperature lower than Stage I but higher than Stage III. After the nearly-mature or fully-mature pseudobulbs with flower buds inside, have been exposed to lower night temperatures for a while, spikes appear, emerging as cone-like nubs (similar to new growths but rounder) from the base of pseudobulbs or within the lowest leaf axils. These enlarging flower buds have been developing in the healthy new growths will eventually become the inflorescences. This is the period when growers can manipulate spike maturation and alter how long it will take before they bloom. In a protected environment where temperature, light, water and fertilizers can be fully controlled, the timing of blooming is partly controllable. The same varieties when grown in different conditions can be made to bloom over an extended period. The group that received the lower night temperature earlier will initiate flower spikes before other plants of the same clone. This can give an advantage over nurseries located in warmer places, with nurseries located at higher latitudes or at higher elevations experiencing earlier blooming.

Because both HTC and WTC have temperature trigger points of flower spike initiation higher than those of conventional/standard cymbidiums, they do not have to wait for the night temperatures to drop as low as the conventional/standard cymbidiums require. If HTC and WTC are grown alongside with conventional/standard cymbidiums, HTC will initiate their spikes first, followed by WTC and concluding with the conventional/standard cymbidiums. This indicates that nurseries located in warmer places or at lower elevations that grow HTC and WTC can have blooms no later than those that grow conventional/standard cymbidiums in cooler places or at higher elevations.

Stage III: Spike elongation and blooming

This stage is the most critical and requires maximum night temperature lower than both Stage I and II. When night temperature keeps dropping continuously and the days get milder or cooler, the flower spikes elongates. Each flower bud enlarges and finally blooms. Depending on the overall temperature profiles, it normally takes at least 30-60 days from when the new flower spikes reach to the full bloom. In case that the autumn cooling is not stable, and especially if the night temperatures are not low enough, problems in spike development become obvious. For example, the elongation may actually slow down, the lateral sepals become deformed, colours lose their intensity, pollen does not attain maturity and may darken, or at worst, the whole spike turns yellow and abort. Normally, cymbidiums with larger flowers and taller upright spikes need lower temperature. They are more susceptible to bud drop due to heat stress than the varieties with arching or pendulous spikes and smaller flowers. Simply, the cut-flower varieties with the largest flowers and tallest spikes require cooler conditions during spike maturation than other varieties. HTC and WTC help in reducing the problem of bud drop if the night chill is not stable and also in the higher temperatures plants frequently face during transportation and display in the city markets.

Conclusions & Extensions
Cymbidium nurseries that most quickly complete the three stages will have the blooms first and no problems with barren pseudobulbs. At every stage, the cool-growing/conventional cymbidiums require lower temperatures than HTC and WTC do.

However, all cool-growing/conventional cymbidium hybrids do not require any temperature as low as 10^{o}C at any growth stage. In reality, many cymbidium nurseries, especially those that produce cut flowers, are located in climates where external winter temperature drop to lower than 10^{o}C at night throughout the whole of stage III. In addition, almost all of the cut-flower nurseries are located in a greenhouse or controlled environment because this is necessary for providing warmth and the stable temperatures desirable during stage III.

Colombia and Ecuador are the two countries in equatorial zones that currently successfully grow cut-flower cymbidiums because they have plenty of suitable growing area at higher elevations. Cut-flower varieties are grown at 2600-2800 metres in Ecuador and above 1600 metres in Colombia. In these equatorial regions, the crops are not seasonal but grown round the year. There are also enthusiasts of orchids and some new commercial nurseries growing cut-flower cymbidiums in northern India (Sikkim, elev. 1200-1400 metres) and China (Yunnan, elev. 1900 metres). These two places are located at lower elevations than Ecuador and Colombia because both Sikkim and Yunnan are located further away from the equator. In Sikkim, they experience the cold air mass flowing down from the snow-capped Himalaya which provides a significant night temperature drop.

Orchid Pseudobulbs - A Genuine Importance in Orchid Growth and Survival
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. Pseudobulbs are also found in some terrestrial orchids like *Cymbidium*, *Eulophia* and *Spathoglottis.*

Orchid pseudobulbs are of two types: heteroblastic or homoblastic. Heteroblastic pseudobulbs consists of only one internode, e.g. *Oncidium*, *Cattleya* and *Miltonia.* Homoblastic pseudobulbs consist of two or more internodes, e.g. *Eria* and *Dendrobium* (Arditti, 1992*).* A number of aspects have been studied in orchids, e.g. mineral nutrition (Hew and Ng, 1996), respiration (Hew, 1987), photosynthesis (Hew *et al*, 1997, Hew and Yong, 1994), flowering (Gow *et al*, 1982), flower physiology (Avadhani *et al*, 1994) and more recently, photo-assimilate partitioning (Yong and Hew, 1995a, Yong and Hew, 1995 b, Yong and Hew, 1995c, Ng and Hew, 1996).

Pseudobulbs -As Water Storage Organs
Orchid pseudobulbs serve as important water storage organs. The epiphytic biotope is characterized 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 adverse climate. Pseudobulbs of *Oncidium* 'Goldiana' maintain relatively high water contents of 90–95% throughout development. In *Stanhopea* and *Pleione,* pseudobulbs are made up of an abundance of water-storing cells (Arditti,1992). In addition, most orchid pseudobulbs possess a thick cuticle that are totally impervious to water and gases. In *Cymbidium sinense* pseudobulbs are able to retain about 64% of their water content after 42 days of water stress conditions (Zengh *et al*, 1992).

Pseudobulbs -As Mineral Storage Organs
Epiphytic orchids faces frequent periods of nutrient scarcity. They can tolerate 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 is a net accumulation of nitrogen and phosphorus with age. In contrary, potassium content decreases with age, indicating that potassium is remobilised to support the growth requirements of new developing tissues (Davidson, 1960).

In *Oncidium* 'Goldiana', uptake of nitrate is reported highest during the formation of new pseudobulbs. In addition, it is observed that mineral allocation to pseudobulbs within connected shoots of *Oncidium* 'Goldiana' is most active during formation and development of a new pseudobulb (Hew and Ng, 1996). There are remarkable reductions in the mineral content of mature pseudobulbs of connected shoots during the development of a new shoot. 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 keep 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.

Pseudobulb Photosynthesis
Photosynthesis is the process by which 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. Experimental evidences 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. 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 within the tissue of the pseudobulb for carbon fixation are ribulose-1,5-bisphosphate carboxylase/oxygenase and phosphoenolpyruvate carboxylase. 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 for those orchids with rudimentary leaves (Winter *et al*, 1983).

In the CAM orchid, *Laelia anceps*, photosynthesis of leaves is largely affected by irradiance of the pseudobulb (Ando and Ogawa, 1987). Exposure of the pseudobulb to light is 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 still unknown whether pseudobulbs of C_3 and CAM orchids have a regulatory role in leaf photosynthesis.

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

Volume : 3 | Issue : 12 | December 2014 • ISSN No 2277 - 8179

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.

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). 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 utilized to meet the increased demand for carbon during inflorescence and new shoot development. This observation explains the need for at least two connected back shoots for optimal inflorescence development (Yong and Hew, 1995b, 1995c).

The Absence of A 'Flag' Leaf – an Apparent Anomaly due to the Pseudobulb

A 'flag' leaf is the main leaf responsible for supplying carbon to the organ of economic importance. This is usually the leaf subtending the economically important organ. 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 indicates that the leaf subtending the inflorescence is the 'flag' leaf. However, radioactive carbon tracer studies have shown an absence of a 'flag' leaf in *Oncidium* Goldiana. All mature leaves within a single shoot supplies similar amounts of carbon to the inflorescence (Yong and Hew, 1996). This apparent anomaly between gas exchange studies and radioactive tracer studies is interesting.

Radioactive tracer studies have shown 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 is no net accumulation of carbohydrate during inflorescence development (Hew and Ng, 1996). Taken together, these results indicate 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 is 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 redistribution 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 research works needs to be done to substantiate the possible regulatory role of pseudobulbs in partitioning of assimilates in orchids.

Pseudobulbs and Myrmecophily

Ants, are in frequent contact with epiphytic plants. 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 characterized 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). Species classified as ant-house orchids include *Caulathron*, *Dimeranda* and *Schomburgkia* while *Vanilla planifolia* has been reported to be an ant-garden orchid. There is evidence to suggest that in both ant-house and ant-garden epiphytes, the ant-epiphyte association is mutualistic. In the CAM orchid *Schomburgkia humboldtiana*, leaves grow from a large hollow pseudobulb and contains ant-nests (Griffiths *et al*, 1989). However, it appears that the hollow pseudobulb of *Schomburgkia humboldtiana* forms spontaneously without excavation by ants. This appears likely to be the result of co-evolution although the actual relationship remains to be unequivocally determined.

The occurrence of an ant-house in pseudobulbs of *Schomburgkia* provides an interesting material for the physiological role of the pseudobulb. It is unlikely that pseudobulbs of *Schomburgkia* are important in water storage like other orchids. 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.

Cattleya is a epiphytic plant generally found growing on trees of moist and wet forests from sea level to 4,900 feet (1,500 m) in elevation. Several published scientific studies have shown that flowering of *Cattleya* species and hybrids is promoted by exposure to short daylengths and cool temperatures. For example, in *Cattleya warscewiczii, Cattleya gaskelliana* and *Cattleya mossiae,* flower induction occurred only when plants were placed under photoperiods of nine hours (nine hours of light per day) at 13ºC, while flowering was inhibited under 16 hours of light per day at 55 ºF (Rotor, 1959).

Dendrobium is one of the largest genera and are native to tropical and subtropical Asia, Australia and various Pacific Islands. The optimum temperature for flower induction consequently differs among *Dendrobium* selections. In *Dendrobium nobile,* plants exposed to a constant 13ºC produced flowers regardless of the daylength, whereas plants placed at 18ºC remained vegetative and did not flower (Goh and Arditti, 1985). In contrast, *Dendrobium phalaenopsis* requires short day lengths and warmer temperatures for flowering. For example, flower-bud development and flowering of plants placed under nine-hour day lengths at 18ºC are accelerated by six weeks compared with plants placed under longer day lengths at the same temperature. A similar response is observed at 13º C, but flower bud development is slower due to the cooler temperature.

Most *Phalaenopsis* species and hybrids require a period of exposure to relatively cool temperatures less than 28ºC to trigger the elongation of the spike (Lee and Lin, 1984, Wang, 1995). Uniform spiking can be achieved when plants are grown at day/night temperatures of either 25/20º C or (20/ 15ºC) for four to five weeks. When induced plants are placed at high temperatures (greater than 28ºC), a spike can form a vegetative air plantlet, known as a keiki, instead of flower buds, or buds may abort. A few experimental evidences have reported that short days enhance spiking and long days promote vegetative growth or the development of keikis in *Phalaenopsis* (Rotor, 1952; Griesbach, 1985). However, this short-day enhancement is thought to be a result of the extension of cool-night temperatures and not the daylength itself. Thus, it appears that photoperiod does not influence flowering of *Phalaenopsis* (Baker and Baker, 1991)

WHAT THE FUTURE HOLDS In recent years, orchids have become the second most valuable potted flowering plant in the United States, with a wholesale value of US $127 million in

2004. More than 12.7 million orchids were sold in the United States last year, with *Phalaenopsis* accounting for more than 75 percent of sales. Why are so many *Phalaenopsis* being sold and purchased when there are well over 25,000 described species of orchids from which to choose? One reason is that we understand how to regulate the flowering process. As mentioned earlier, growers can prevent flowering by maintaining the day and night temperatures above 82 F (28^{o} C). To induce flowering, plants need to be grown at cooler temperatures. Unfortunately, there is virtually no adequate information available on the flowering of many other orchids, such as *Miltonia*, *Oncidium*, *Vanda*

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