International Journal of Bio-resource and Stress Management https://pphouse.org/ijbsm.php

IJBSM November 2022, 13(11):1312-1322 Print ISSN 0976-3988 Online ISSN 0976-4038 **Article** AR3115a

Review Article *Natural Resource Management*

DOI: HTTPS://DOI.ORG/10.23910/1.2022.3115a

Adaptational Mechanisms of Epiphytic Orchids: A Review

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ABSTRACT

Orchidaceae belongs to the 84 families of vascular plants that cover species following the epiphytic life pattern. Adaptations are specialized mechanisms that permit a plant or animal to live in a particular area or habitat. Adaptational mechanisms in plant morphology are essential for the transition to an epiphytic canopy habitat. Orchids have specific adaptational mechanisms in the roots, stems, leaves, flowers, seed and other physiological processes. Under water scarcity, these orchids have developed pseudobulbs, an energy, water, and nutrient storage bulb for adaptations.A wax coating covering the surface of the leaf, also prevents evaporation and gas exchange in drier or hotter climate.Epiphytic orchids have adequate root systems to enable them to grow in a poor nutrient environment when they grow at slow rate. In such cases, velamen of orchids helps to absorb water and also help to absorb nutrients from rainfall. Orchid roots are adapted to cling to trees. Orchid seeds do not have endosperm and require a fungal association with mycorrhiza to provide its energy till the development of roots and leaves. This symbiotic feature is another adaption to make the orchid seed to travel longer and further distances for survival. In comparison to the activity of C_3 photosynthesis, crassulacean acid metabolism (CAM) in many epiphytes plays a vital role in improving carbon gains and water use. In this review, specialized adaptations of some commercial orchid genera namely Dendrobium, Cymbidium, Phalaenopsis, Cattleya, Oncidium, Epidendrum and Paphiopedilum are discussed in detail.

KEYWORDS: Adaptations, CO_2, crassulacean acid metabolism, C_3 orchids, velamen

Citation* (VANCOUVER)*: De and Biswas, Adaptational Mechanisms of Epiphytic Orchids: A Review. *International Journal of Bio-resource and Stress Management,* 2022; 13(11), 1312-1322. HTTPS://DOI.ORG/10.23910/1.2022.3115a.

Data Availability Statement: Legal restrictions are imposed on the public sharing of raw data. However, authors have full right to transfer or share the data in raw form upon request subject to either meeting the conditions of the original consents and the original research study. Further, access of data needs to meet whether the user complies with the ethical and legal obligations as data controllers to allow for secondary use of the data outside of the original study.

Conflict of interests: The authors have declared that no conflict of interest exists.

RECEIVED on 02nd June 2022 RECEIVED in revised form on 24th October 2022 ACCEPTED in final form on 14th November 2022 PUBLISHED on 28th November 2022

1. INTRODUCTION

Adaptations are specialized mechanisms that allow a plant or animal to live in a particular locality or habitat. These adaptations could make it very difficult for the plant to survive in a different place. There are three types of plant adaptations: structural adaptations, behavioral adaptations, and physiological adaptations. Structural adaptations are the physical mechanisms, which permit them to compete. A spectacular example of such type is the formation of spines in cacti and roses that can stop a plant being grazed by animals. Behavioral adaptations are actions that a plant takes in order to increase its chance of survival. An example of a behavioral adaptation in plants are tropisms. A physiological adaptation is an internal process that increases a plant›s chance of survival. One example of a physiological adaptation seen in plants is the creation of poison for defense.The family Orchidaceae have derived as terrestrial forest understory herbs approximately 100 million years ago (Chase et al., 2001). Orchidaceae belongs to the 84 families of vascular plant families that cover species following the epiphytic life pattern. Among flowering plants, orchids are the second largest families (Willis, 2017))with most diverse groups of angiosperms in terms of floral form, size, shape, colour and fragrance with nearly 25,000–30,000 species belonging to 750–800 genera (Crain and Tremblay, 2014, Zhang et al., 2018). The family orchidaceae comprises of five subfamilies namely *Apostasioideae*, *Cypripedioideae*, *Vanilloideae*, *Orchidoideae*, *Epidendroideae*. Orchidscover about 8% of angiosperm species diversity (Chase et al., 2015). According to Govaerts et al. (2017), 29,199 species have been identified and accepted although several hundred new species are added each year. Botanically, orchids are monocot plants. They could be of epiphytic, terrestrial and lithophytic. Globally, orchids are epiphytic and/or lithophytic (70%), terrestrial (20%) and both lithophytic, epiphytic and terrestrial accounting to 5% (Arditti, 1992). Epiphytic orchids are usually characterized by succulent leaves with thick cell walls, cuticles and sunken stomata whereas terrestrial orchids possess rhizomes, corms or tuber. They have a long juvenile period, slow growth rate. Epiphytic orchids are known to adapt semi-arid habitat with periodic drought by utilizing Crassulacean acid metabolism (Silvera et al., 2010, Kerbauy et al., 2012, Yang et al., 2016). Orchids with succulent leaves such as Bulbophyllum, Phalaenopsis are characteristic of CAM expression (Yam, 2013, Yong et al., 2015), while thin leaved orchids such as Coelogyne, Arundina fix carbon primarily through C_3 pathway (Hew and Yong, 1994). The expression of C_3 intermediate species varies with experimental conditions such as photoperiod, light, temperature, atmospheric carbon dioxide concentrations, drought and salinity (Winter and Holtum, 2014, Oh et al., 2015, Nosek et al., 2018). Drought tolerant plants may also accumulate different solutes in the cytosol to lower osmotic potential and maintain cell turgor (Hosseini et al., 2018, Kozminska et al., 2018). Another adaptive mechanism of orchids to drought is the accumulation of proline in plants, a common physiological response to abiotic stresses (Ings et al., 2013, Kaur and Asthir, 2015) adapting to adverse climatic conditions including osmoregulation in drought tolerance (Yang et al., 2015, Blum, 2017). During drought greater use efficiency is achieved through osmoregulation, regulation at stomatal level to reduce transpiration water loss (Fang and Xiong, 2014). In C_3 epiphytic bulbous orchids, pseudobulbs play important role in storage and supply of water (He et al., 2013, Yang et al., 2016). Keeping in views, the reviewed paper has been aimed to explain the detailed morphological, anatomical, physiological and biophysical mechanisms of adaptations of epiphytic orchids.

2. HABITAT ADAPTATIONS

Globally, tropical orchids comprise of more than 1200 species of Dendrobiums, more than 50 species of Vanda, more than 40 species of Cattleyas and more than 300 species of Oncidiums. Only few species grow in soil, but the majority of them grow on trees or rocks. Majority of orchid species have originated from the wet and warm rainforests of Asia, Australia and South America. The rainforests of the world provide the suitable environment Specifically filtered sunlight to bloom. Vandas need more amount of light because of their small shaped leaves. Dendrobiums, Cattleyas and Oncidiums like partially shady locations.

Tropical epiphytes have come across a very harsh life at certain times of the year. Even in the rainforest, they have to perform days or weeks without water and subsequently they have to shed their leaves and stems. The roots have an actively growing tip with the older parts being covered in an envelope of dead empty cells. The tip protects the inner tissues which help in the uptake of moisture from the atmosphere. This can have a blotting paper effect for the orchid.

3. CLIMATIC ADAPTATIONS

3.1. Light

A universal style of light requirement exists for individual species of orchids. The photosynthesis and growth of most orchids demand a low level of irradiance because they live in forests (Zhang et al., 2007, Chang et al., 2011). Myco-heterotrophic orchid species acquire carbon through heterotrophic exploitation of mycorrhizal fungi and are usually light-independent.Although these plants contain a certain amount of photosynthetic pigment, e.g., chlorophyll

(Chl) a and xanthophylls but they are photochemically ineffective (Cameron et al., 2009). Species with Different habitat also show different requirements for light. For example, *Cymbidium tracyanum*, harbouring in the tree canopy is more tolerant of high irradiance than the closely related *Cymbidium sinense* occurring on shady forest floors (Kuang and Zhang, 2015). When light intensity exceeds the amount requires for photosynthesis, e.g., after seasonal leaf-shedding by the host tree in a tropical dry forest, epiphytic orchids in the newly exposed canopy show considerable photoprotective plasticity to cope with such stress (Rosa-Manzano et al., 2015).

Orchids also have different light requirements at various stages of development after germination. For Phalaenopsis hybrids, a stomatal opening is influenced by specific blue light during photosynthetic induction (Zhang et al., 2018). Red or far-red light usually enhances the vegetative growth of seedlings in flask or green house cultivation, whereas blue light improves production of chlorophyll (Islam et al., 1999). Like other plants, orchids are also classified into short-day, long-day, or day-neutral (Hew and Yong, 2004). The effect of photoperiod on vegetative growth of orchids is species-specific, and species and hybrids within a genus may have different responses. Some orchids need a short day for flower initiation, whereas other species of Cymbidium and Phalaenopsis, show no response or an ambiguous response to photoperiod depending upon the impact of growth temperature (Lopez and Runkle, 2005). The system of night interruption can be applied to induce flowering by long-day orchids and improve flower quality in commercial cultivation (Kim et al., 2011).

3.2. Temperature

The orchid often responds to an optimum temperature at which the growth rate at maximum level. Temperatures that exceed either end of that optimum range may show a negative effect on growth and development. For example, night-time CO_2 absorption by Phalaenopsis is inhibited at temperatures above 25°C or below 15°C (Arditti and Pridgeon, 1997).

Tropical or sub-tropical orchids tend to be more sensitive to chilling stress and genera such as Phalaenopsis hardly survives in regions where severe, long-term chilling prevails at natural condition.Low temperatures may cause many stress symptoms such as leaf-yellowing, leaf –pitting, defoliation, or a slow growth. At these temperatures, mature leaves are more tolerant than young leaves (Sheehan and McConnell, 1980). Anatomical studies have indicated that pitting is due to the mesophyll cell collapse, found initially in cells between the large vascular bundles. Intense damaged areas are recognized by extensive collapse of cells surrounded by hypertrophical cells (Sheehan, 1983).Plants can show lower rate of photosynthesis at low temperatures due to the reduction of Rubisco activity and RuBP regeneration. In evergreen orchids that exhibit higher temperature homeostasis of photosynthesis, some species like Pleiones and Bletilla, may have an escape strategy by up-regulating photosynthetic efficiency and fixing more carbon during the hot season followed by shedding of leaves and roots, leaving a dormant pseudobulb to survive in the cold temperatures (Cribb and Butterfield, 1999).

Moderate high temperatures generally enhance plant growth, but extremely high temperatures can hinder physiological activities. At high temperatures cellular membranes and ions become weaken and tissue necrosis occurs (Jones, 1992).

When orchids are shifted from alpine habitat to a tropical habitat, their leaves show reduced rate of photosynthesis, stomatal conductance, transpiration, and carboxylation efficiency.Reduced g values measured at that tropical habitat can suppress the diffusion of CO_2 into the leaf, which further exacerbates the depression of photosynthetic capacity (Zhang et al., 2005). When plants are subjected to above optimal photosynthetic temperature, their photosynthetic rates are retarded while that of respiration continues to increase. This may cause to an imbalance glutathione peroxidase, and glutathione-S-transferase in the leaf and root; glutathione reductase in the leaf; and guaiacol peroxidase in the root are induced significantly at 40°Crather than at 25°C, suggesting that these enzymes have impact onthermal protection (Mohammad et al., 2005).

In Dendrobium, flower emergence only occurs when mature pseudobulbs are subjected to temperatures of 7.5°–20.0°C. Cool rain may induce the flowering of these orchids in their natural habitats by decreasing temperatures. Temperature signals generally affect floral development and morphogenesis by influencing hormone levels (Arditti and Pridgeon, 1997). In *Phalaenopsis hybrida*, the temperature regulation relies on an optimal level of endogenous gibberellin in the tip of the flowering shoot. Such shoots contain a lower amount of the hormone when grown at 30/25°C (day/night) than at 25/20°C (Suet al., 2001). These experimental evidences have been used to develop strategies for commercial cultivation of orchids. For example, temperature manipulation is applied to control and synchronize flowering time in Cymbidium, Dendrobium, and Phalaenopsis (Chen et al., 1994, Hew and Yong, 2004).

4. MORPHOLOGICAL ADAPTATIONS

Adaptations in plant morphology are essential for transition to an epiphytic canopy habitat. Orchids have shown specialized adaptations in the roots, stems, leaves, flowers, seed and other physiological processes. Epiphytic orchids do not have any vascular connection to the host tree. The host only assist in a habitat that has more sunlight than the forest floor. Orchids are capable to absorb required nutriments from the surface of the host and rainwater.

4.1. Roots

Orchid roots play important role in anchorage for the plant, photosynthesis, and water and nutrient uptake and storage.These adventitious roots usually develop from the rhizome.Orchid roots exhibit a spongy layer of cells outside the exodermis known as the velamen that functions as temporary water storage (Pridgeon, 1987). These cells can absorb rainwater along with nutrients rapidly and hold it until it can be translocated across the exodermis into the vascular system. Roots of epiphytic orchids are exposed to the light and the root cells have functioning chloroplasts. Orchid roots have capacity to process sunlight and transform it into energy. From full sun to full shade and everything in between orchids have modified their anatomical structure to survive in each habitat in a better way.

4.2. Pseudobulbs

Epiphytic orchids often have called pseudobulbs, enlarged portions of the stem which are used for storage of water and carbohydrate. Orchid pseudobulbs may be of two types: heteroblastic or homoblastic. Heteroblastic pseudobulbs containonly one internode, e.g. Oncidium, Cattleya and Miltonia. Homoblastic pseudobulbs have two or more internodes, e.g. Eria and Dendrobium (Arditti, 1992). The epiphytic biotope has to pass over the frequent periods of water and nutrient shortage. Presence of fleshy organs in roots, stems or leaves provides epiphytic orchids the ability to survive and grow in adverse climate. Pseudobulbs of Oncidium 'Goldiana' maintain relatively high water contents of 90–95% throughout developmental stages. In *Stanhopea* and *Pleione*, pseudobulbs are consisted 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 may retain about 64% of their water content after 42 days of water stress conditions (Zheng et al., 1992). In *Oncidium* 'Goldiana', uptake of nitrate is reported highest during the formation of new pseudobulbs. Besides, it is found that mineral allocation to pseudobulbs within connected shoots of Oncidium 'Goldiana' is most active during formation and development of a new pseudobulb (Hew and Yong, 2004). 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 available 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*. In the CAM orchid, *Laelia anceps*, photosynthesis of leaves is largely influenced by irradiance of the pseudobulb (Ando and Ogawa, 1987). Exposure of the pseudobulb to light is required for leaves to carry outdaily 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 increased by exposure of the pseudobulb to light. It assumes 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 not available. Studies on both *Catasetum viridiflavum* (Zimmerman, 1990) and *Oncidium* 'Goldiana' (Hew and Yong, 2004) have revealed 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 spike development. Pseudobulbs may be cylindric, clavate, globular in *Cattleya*; narrow cylindric, round, ovoid, conical in *Cymbidium* (Figure 1); cane woody, cane cylindric fleshy, cane clavate fleshy, bulbous round in *Dendrobium* (Figure 2) and oblong, elliptic, ovate and grooved in *Oncidium* (De, 2021).

4.3. Leaf

Epiphytic orchids have thick and succulent leaves with thick cell walls, cuticles and small substomatal chamber whereas those of terrestrial species are thin. Usually, mature leaves exhibit active photosynthetic rate. Leaves are considered as sites for reduction of transpiration, water storage organs, retention of rain or condensed water and

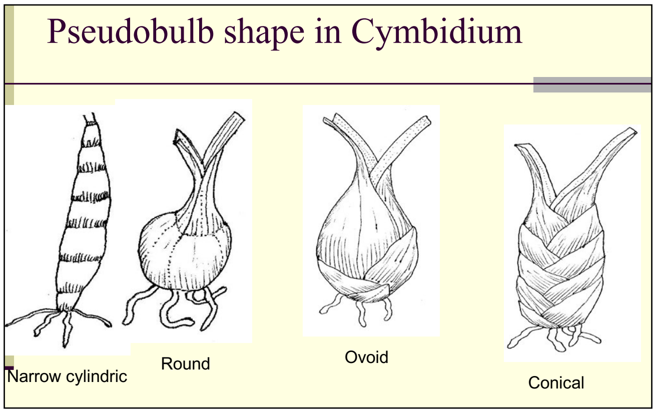

Figure 1: Pseudobulb shape in Cymbidium

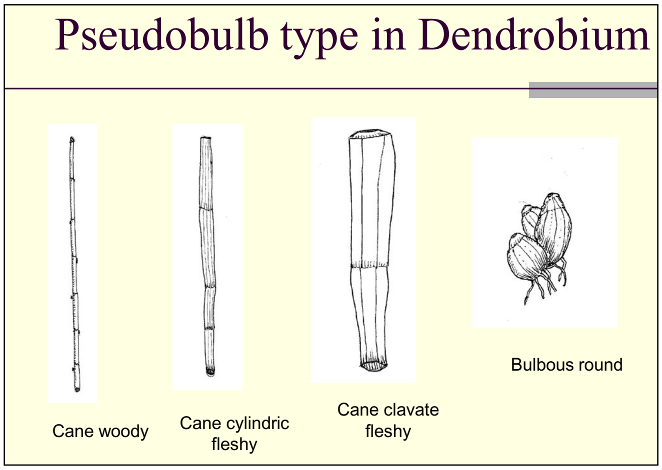

Figure 2: Pseudobulb shape in Dendrobium

absorption of water as liquid or vapour. The hard leathery leaf type of orchids are drought tolerant due to theirvery thick cuticle and thick-walled epidermis together with extensive lignification offering excellent protection against desiccation. Thick leaves exhibit 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 broader ones because they lose heat more efficiently by convection. Leaf hair may assist to conserve water by increasing the boundary layer thickness of air around the leaf and lengthening the diffusion pathway. Under dry climate, orchid leaves adapted to trap in humidity. Deciduousness occurring in sympodial orchids avoid water stress during the dry season by shedding their leaves and entering a dormancy period. In Ghost orchid, *Dendrophylax lindenii* the plants are leafless and do not contain chlorophyll. They are not capable of doing photosynthesis and obtain all kinds of nutrients from fungal association. In monopodial orchids, the number of leaves on stem depends on the age of the plant while the orchid like *Cattleya* has 1 leaf pseudobulb^{-1} and *Dendrobium* has 5–20 leaves pseudo bulb^{-1}.

4.4. Flower

Orchids are monocotyledonous plants bearing flowers with seven floral parts- three sepals, three petals and the column or gynostemium. The orchid flowers can have a great diversification in size, colours and shape. The range of size varies from that in some species of *Oberonia* (0.15cm across) to *Pecteilis gigantea* (10 cm across). The predominant colours are white, yellow, green and purple occurring in pure state or shades or in every possible combination. The orchid flowers exhibit mimicry like Spiders, Dancing girls, Bees, Ladies slipper, or Insects. In few cases like *Oberonia* and *Malaxis* the flowers are in an upside-down position, having twisted through 180° on its pedicel. 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. It is called resupination. Some orchids have secondarily lost this resupination, e.g. *Zygopetalum* and *Epidendrum secundum*. The inflorescence of *Geoderum densiflorum* bends down in 180° and present the flowers in upside down position. One of the most important characteristics of all orchid flowers is that they are zygomorphic and bisexual or very rarely unisexual. The orchid flowers may have or have not spur which is the appendage of lip meant for storing nectar. It may be short or long in size and vary in shape. The orchid flowers consist of three outer most floral parts- the sepals are more or less similar in appearance. But in few cases like *Bulbophyllum*, the dorsal sepal is of different size from the laterals. They may be coloured (petaloid sepals) and free from one another or united forming sepaloid tube. The inner whorl of three segments called the petals. The two lateral petals are alike and the other one, called the lip or labellum, is highly modified and enlarged (Brown, 2005). The labellum is the most prominent and distinctive part of the orchid flower. The petals may be similar to sepals and are filiform or fimbriate. The lip is attached to the base of the column loosely or firmly. The colour pattern, size and shape of the lip vary in different genera. The most fascinating aspect of the lip is its habit of mimicry to facilitate pollination.

The column or gynostemium is located at the center of the flower, is the unique structure distinguishing the orchids from all other kinds of plants. It is the reproductive part of the flower formed by the union of the male (anther) and female organs (stigma) (Roberts and Dixon, 2008). It bears one to three movable or rigidly attached anthers at its tip or on the sides. On the basis of one or more fertile anthers, orchids are called as Monandrae or Pleonandrae, respectively. The anther contains a mass of pollen called pollinium which is varying from 2, 4 and 6 to 8. The Pollinia are contained in a cavity called the clinandrium. Just below the anther, on the ventral surface of the column, is a hollow cavity of sticky and viscid mass known as stigmatic surface. It is formed by the fusion of two fertile stigmas. The anther and stigmatic surface are separated by the structure called rostellum, which is actually the third stigma. The rostellum serves to prevent from self-pollination. The genera like *Eria* and *Dendrobium*, the column is extended below into a structure called foot. The orchidaceous ovary is generally inferior, tricarpellary, one-celled, with numerous numbers of ovules on 3 parietal placentas. It is stalked or sessile.

4.5. Seed

Seeds of orchid are generally adapted for wind disbursal. The dust like seed consists of a tiny embryo and a net like testa.The seed does not contain endosperm, the 3N tissues that basically feed a developing embryo. In orchids, during germination a mycorrhizal fungus penetrates the testa and feeds the embryo (Rasmussen, 1995). This symbiotic relationship is another spectacular adaption so the orchid seed could travel longer and further distances for survival.

5. PHYSIOLOGICAL PATHWAYS

Most of the vascular epiphytes occurring in tropical and subtropical regions normally grow on tree trunks in forests and/or on rock surfaces in valleys (Benzing, 1990). Unlike terrestrial plants, their roots have no contact with the soil. Therefore, water stress is a major limitation factor to their survival, growth and distribution (Zotz and Hietz, 2001, Laube and Zotz, 2003, Zotz and Bader, 2009). However, vascular epiphytes are more drought tolerant than terrestrials (Rada and Jaimez, 1992, Watkins and Cardelus, 2012, Zhang et al., 2015), although the water-adaptive strategies differ among epiphytic species.

Under water scarcity, vascular epiphytes exhibit morphological and anatomical adaptations in their leaves, stems and roots, including thickened cuticles, stomata surrounded by trichomes, a reduction in transpiring surface areas through sympodial growth, and development of aerial root systems (Moreira et al., 2013) (Table 1). The leaf cuticles of vascular epiphytes serve as efficient barriers against water loss after their stomata close (Helbsing et al., 2000).Furthermore, these types of epiphytes have greater ability for foliar water uptake and tend to have thinner hydrenchymal and cuticle layers (Gotsch et al., 2015). Other mechanisms for storing water are succulent leaves and pseudobulbs, which are common features in vascular epiphytes (Sinclair, 1984, Zimmerman, 1990). The hydrenchyma in succulent leaves from several epiphytes can store water to buffer the effects of reduced water supplies during drought periods (Zotz and Bader, 2009, Ogburn and Edwards, 2010).

A modified photosynthetic pathway as an adaptation of orchids to the dry canopy habitat. The stomatal opening to take up carbon dioxide is always connected with large losses of water.To inhibit this loss, Crassulacean Acid Metabolism (CAM) involves a process that allows the uptake of carbon dioxide during the night when relative humidity is higher than during daylight periods. The prefixed carbon dioxide is stored in vacuoles and is utilized during the daytime for photosynthesis. When compared with the performance of C$_3$ photosynthesis, crassulacean acid metabolism (CAM) in many epiphytes plays a vital role in improving carbon gains and water use (Motomura et al., 2008). Furthermore, the CAM pathway of photosynthesis can enable plants to harvest external CO$_2$ at low cost of water (Reinert, 1998, Lüttge, 2004). Thick leaved vanillas, aerides, aranda, cattleyas and phalaenopsis use CAM metabolism while thin leaved oncidiums, bamboo orchids often use the more conventional photosynthetic pathways (Gilberto et al., 2012).

Table 1: Morphological and physiological adaptations of epiphytic orchids

Morphological traits	Role	Habitat differences
Leaf		
Mass of Leaf unit^{-1} area	Water availability andenergy exchange	Epiphytic>Terrestrial
Leaf thickness	Water availability	Epiphytic >Terrestrial
Leaf epidermal thickness	Water conservation	Epiphytic>Terrestrial
Degree of leaf succulence	Water conservation	Epiphytic>Terrestrial
Epidermal conductance	Water loss	Epiphytic<Terrestrial
Water loss rate	Water balance	Epiphytic>Terrestrial
Vessel diameter	Water transport	Epiphytic>Terrestrial
Crassulacean acid metabolism	Water utilization	Epiphytic species only
Pseudobulb		
Relative water content	Water conservation	Epiphytic>Terrestrial
Ratio of leaf area to pseudobulb dry weight	Water balance	Epiphytic>Terrestrial
Area of water storage cell	Water storage	Epiphytic>Terrestrial
Root		
Velamen radicum	Water and nutrient uptake	Epiphytic orchids Only
Ratio of velamen radicum thickness to root semi-diameter	Water and nutrient uptake	Epiphytic>Terrestrial
Number of xylem conduit	Water transport	Epiphytic>Terrestrial

Source: Zhang et al. (2018)

6. NUTRITION

Epiphytic orchids can survive in a poor nutritional environment. Dust settling on leaves, nutrients in the atmosphere and molecules leached from leaves by dripping rainfall supply most nutrients taken up by the epiphytes in dissolved conditions. Orchids develop specialized root systems to enable them to grow in a poor nutrient environment as long as they grow at slow rate.In such cases, velamen of orchids helps to absorb water and also help to absorb nutrients from rainfall. However, the main source of nutrients is the slow decomposition of organic matter that accumulates in the tree crotches and among the bark, roots, rhizomes and roots of the orchid plants (Poole and Sheehan, 1982). Epiphytic orchids are adapted to ecological constraints with unique mechanisms that tap limited resource pools, prolong contact with passing canopy fluids and promote water and nutrient use efficiency. Epiphytic orchids are adapted to the water deprived and nutrient deficient environment by growing more slowly, producing leaves that are thick and hard and diverting more energy into root formation. A greater air movement in the tree canopy helps to dry leaves rapidly after storms which prevent bacteria and fungi from penetrating into the plants. Abundant air movement, diffused light, porous potting mixtures will help to grow healthy plants which subsequently produces lots of blooms.

7. ADAPTATIONS IN SOME COMMERCIAL ORCHID GENERA

7.1. *Dendrobium*

The morphological as well as anatomical studies in *Bulbophyllum* and *Dendrobium* (Orchidaceae) on ecological adaptation and phylogenetic implications have indicated that stomata were confined to abaxial surface. The existence of stomatal ledges and substomatal chambers is useful in retarding leaf transpiration and water evaporation. Single- or multi-layered velamen has been foundin both genera. It was reported that tilosomes were always associated with single layered velamen roots whereas completely absent in multilayered velamen taxa (Ramesh et al., 2020). Studies on comparative leaf and root anatomy of two Dendrobium species (Orchidaceae) from different habitat in relation to their potential adaptation to drought have shown there were significant differences on anatomical characters between both species. Compared to *D. arcuatum*, *D. capra* shows more developed anatomical features for adapting to drought and dry condition. These anatomical features were a thicker cuticle, thicker epidermis, presence of hypodermis, thicker mesophyll, broader primary vascular bundle, well developed xylem's sclerenchyma, lower stomatal density, thicker and high proportion of velamen. Yang et al. (2016) revealed that two species (*D. chrysotoxum* and *D. officinale*), with reducing rates of water loss, have thicker leaves and upper cuticles, but lower epidermal thickness and leaf dry mass area^{-1}. In contrast, the other two species (*D. chrysanthum* and *D. crystallinum*) with thinner cuticles and higher rates of water loss, have less tissue density and greater saturated water contents in their pseudobulbs. Therefore, our results indicate that these latter two species may resist drought by storing water in the pseudobulbs to compensate for their thin cuticles and rapid water loss through the leaves. Under the same laboratory conditions, excised pseudobulbs with attached leaves had lower rates of water loss when compared with samples comprising only excised leaves. This implies that epiphytic orchids utilize two different strategies for sustaining water balance: thick cuticles to conserve water in leaves and water storage in pseudobulbs. The results also reveal that *Dendrobium* species with thin cuticles tend to have pseudobulbs with high water storage capacity that compensates for their faster rates of water loss. These outcomes contribute to our understanding of the adaptive water-use strategies in *Dendrobium* species, which is useful for the conservation and cultivation of epiphytic orchids.

7.2. *Cymbidium*

A comparative genomic analysis has shown that *Cymbidium ensifolium* has experienced two whole-genome duplication (WGD) events, the most recent of which was shared by all orchids, while the older event was the τ event shared by most monocots. The results of MADS-box genes analysis did support for establishing a unique gene model of orchid flower development regulation, and flower shape mutations in *C. ensifolium* were shown to be associated with the abnormal expression of MADS-box genes.

The most abundant floral scent components identified were methyl jasmonate, acacia alcohol and linalool, and the genes involved in the floral scent component network of *C. ensifolium* were determined. Furthermore, the decreased expression of photosynthesis-antennae and photosynthesis metabolic pathway genes in leaves was shown to result in colorful striped leaves, while the increased expression of MADS-box genes in leaves led to perianth-like leaves. These results provide fundamental insights into orchid evolution and diversification.

7.3. *Phalaenopsis*

Phalaenopsis or "phals" are the orchid of choice in a home setting. Their thick, waxy leaves can tolerate dry home environment better than others with slender, wispy foliage. Once a phal is blooming, the plant may provide color for four to six months even upto 11 months in a year.

7.4. *Cattleya*

Like other epiphytes, the cattleyas have adapted their structure to meet their requirements. They do not have access to the continuous water supply that terrestrials have on the ground. Therefore, the plants are more dependent on catching rain and dew, and on living only in a high humid region. Most cattleyas have developed storage organs in the form of thickened stems called as pseudobulbs and fleshy leaves, which store both nutrient and water, and protect the plants from drying out between rains.

They able to survive in the airiest and highest regions of the tree canopy. The set of morphological traits of Cattleya leaves suggested the drought-inducible CAM up-regulation as a possible mechanism of increasing water-use efficiency and carbon economy.

7.5. *Oncidium*

Some species have small pseudobulbs with very stiff erect leaves. The leaves are as a water reserve for the plant. There are some equitant oncidiums which do not have pseudobulbs but triangular to oval broad fleshy leaves which again operate as a water reservoir. Under drought, the set of morphological traits of Oncidium belonging to C_3 photosynthesis are supposed to express facultative CAM in its roots and pseudobulbs but not in its leaves, indicating that such photosynthetic responses might compensate for the lack of capacity to perform CAM in its thin leaves. Morphological features of Oncidium leaves also exhibited lower efficiency in preventing water and CO_2 losses, while aerenchyma ducts connecting pseudobulbs and leaves suggested a compartmentalized mechanism of night time carboxylation via phosphoenolpyruvate carboxylase (PEPC) (pseudobulbs) and daytime carboxylation via Rubisco (leaves) in drought-exposed Oncidium plants.

7.6. *Epidendrum*

The anatomical studies have shown that leaves of *Epidendrum radicans* have a thick cuticle (3–4 µm) and paracytic type of stomata. Foliar epidermal cells are found conical on the adaxial surface and rectangular in the abaxial surface, distinct hypodermis absent, and uniseriate fiber bundles are arranged in both sides of the leaves. The foliar mesophyll is homogenous and contain starch grains and raphides. The leaf sheath covering the stem have cuticle restricted to the outer surface and airspaces are prevalent. The stem has a cuticularized uniseriate epidermis and a uniseriate hypodermis. The cortex and a parenchymatous ground tissue of the stem are compartmented by a layer of sclerenchymatous band. Vascular bundles are collateral and their size usually increase from the periphery towards the center. The phloem pole is covered by a sclerenchymatous patch, whereas the xylem is covered by thin-walled parenchymatous cells. The roots have*Epidendrum*-type velamen. Cover cells present. Uniseriated dimorphic exodermis consists of U-thickened long cells and thin-walled passage cells. The endodermal cells O-thickened, pericycle sclerenchymatous, xylem 10–14 arched.The pith is sclerenchymatous, but parenchymatous at the center. The anatomical investigation of *E. radicans* revealed adaptations to moisture stress conditions like thick cuticle covering the leaves and stem, water storage cells, multilayered velamen and dimorphic exodermis.

7.7. *Paphiopedilum*

In these genera, overall, the shape of the leaves, staminodes, and petals, petal width and number of flowers per spike exhibit strong phylogenetic conservatism and distinct evolutionary shift. The flower color character having a weak signal, shows strong convergence, possibly because of a departure from Brownian motion evolution, e.g., adaptive evolution, and less affected by phylogeny, rather than more affected by environment. Flowers of these slipper orchids are thought to be pollinated usually relying upon morphology and scent to attract pollinators (Shi et al., 2009). The lip shape for Paphiopedilum flowers is very important for insect pollination (Shi et al. 2006; Crib, 1998). There are two shapes of lips occur: subglobose/ovate/subsquare or slipper-/helmet- shaped. The former is similar to that associated with the genus Cypripedium, and also found in the species of subgenus Brachypetalum examined here, i.e., *P. bellatulum*, *P. armeniacum*, *P. delenatii*, *P. emersonii*, *P. hangianum*, *P. malipoense*, and *P. micranthum*. These similarities between the flowers of Paphiopedilum and Cypripedium are a result of having similar pollination syndromes that involve bees as pollinators (Cribb, 1987). The subglobose-shaped lip, with involute margins apically, may help prevent access by insects with larger bodies. Members of subgenus Paphiopedilum include *P. parishii*, *P. dianthum*, *P. appletonianum*, *P. wardii*, *P. venustum*, *P. purpuratum*,*P. spicerianum*, *P. insigne*, *P. barbigerum*, *P. tranlienianum*,*P. tigrinum*, *P. charlesworthii*, *P. helenae*, and *P. villosum*, all of which carry helmet-shaped lips that have large, deep mouths but no involute margins. Obviously, this structure is beneficial to prevent smaller-sized insects from escaping. The shift in morphology to helmet shaped lips among species within the Paphiopedilum genus may, therefore, be an adaptation that makes these plants more accessible to pollinators with smaller bodies. Several studies have successfully demonstrated that variation in floral traits among groups is a consequence of adaptation to different pollinators (Shi et al., 2006, Shi et al., 2009). Staminode shape exhibits high morphological diversity within Paphiopedilum, playing an important role in species identification.This particular character shows strong phylogenetic conservatism and may have an important role in luring pollinators. Whereas species under subgenus Brachypetalum have broad and even petals, species within subgenus Paphiopedilum have narrower, more unevenpetals. Variations in leaf types are considered an adaptation to different growing environments and a strategy for reducing damageby herbivores (Givnish, 1979, Brown et al., 1991). The tessellated leaf trait is common in most of the early-diverging species within subgenus Brachypetalum and is absent in most species of subgenus

Paphiopedilum. Tessellated leaves are thought to serve as anti-herbivory camouflage in understory herbaceous plants that grow under sun-flecked light conditions (Givnish, 1990). Most of the species within that genus, whether their leaves are solid green or tessellated, occur in similar shady forest-floor habitats.

8. CONCLUSION

Orchids have a number of specialized adaptations like aerial roots with velamen to absorb water and nutrients from air, pseudobulbs to store water and nutrients for dry periods, waxy or leathery leaves to restrict water loss, masses of pollen to improve the chances of pollination, very light seeds for easy spread, myco-heterotrophic nutrition for easy germination and crassulacean acid metabolism pathways in acquiring carbon gains and water use and to harvest external CO_2 at low cost of water.

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