THE SECRET LIFE OF ORCHID ROOTS

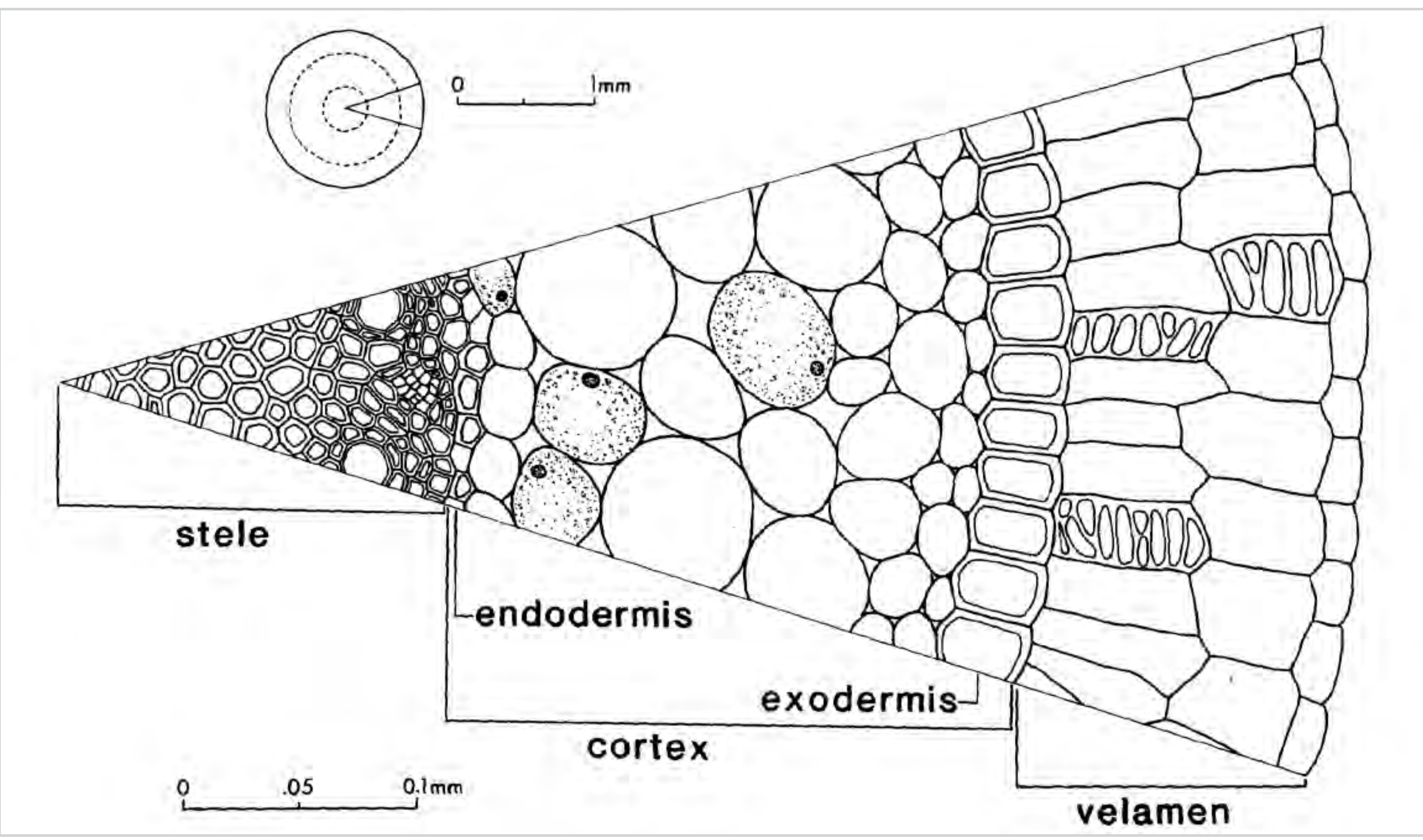
CAROL SIEGEL

There are some four million different kinds of animals and plants in the world.
Four million different solutions to the problems of staying alive.
-David Attenborough

IN CHALLENGING ENVIRONMENTS and hostile conditions, orchids have a tough time staying alive. Wherever they live, they face critical shortages of some elements needed for survival. Growing in leaf litter at the shady base of the forest canopy, they rarely get sufficient light for adequate photosynthesis. Growing precariously on branches at the top of the forest canopy or sitting exposed on a rock, they get plenty of light but are desperate for a secure hold, for water, and for essential nutrients. Yet orchids have not only survived but also thrived to become a dominant life form, representing fully ten percent of all plant species. Against all odds, orchids have figured it out. Orchid roots are one very elegant solution to the orchid's problem of staying alive. Their structure is uniquely adapted to quickly capture and retain water and nutrients, and their velamen cleverly endows the root with survival advantages. Moreover, roots have exploited fungi to provide the plant with whatever the environment lacks. Some orchid roots even provide a home for ants that supplement orchid nourishment. Orchid roots are an amazing adaptation, stunning in complexity and efficiency. This is the secret world of orchid roots.

The Velamen Radicum: A Root Sponge

In most of the plant kingdom, roots are the hidden half of the plant, burrowed deep within the soil. With seventy-five percent of orchids living as epiphytes in tropical rain forests, aerial roots are no longer hidden. They hang down like long beards, freely exposed to the air or sometimes growing along the surfaces to which they are attached. The roots are thick and smooth with a silvery-white color, except for the green growing tip. A spongy, multi-layer of dead, air-filled cells, known as the velamen radicum, covers the root and gives it its distinctive color. During a rain storm, the cells soak up water like blotting paper, becoming transparent, revealing the green core of the root underneath. Unlike most plants, aerial roots have chloroplasts and can perform photosynthesis, helping to provide food for the orchid. The outer layer, the velamen, borders on the inner cortex with an exodermis and endodermis . The velamen commonly has root hairs that increase the surface area for absorption as in *Acianthera pubescens* (syn. *Pleurothallis smithiana*) and aid in anchoring the plant to the substrate as in angraecums and phalaenopsis. The next



Root transection of *Restrepiella ophiocephala* (drawn from a free-hand section).

Angraecum viguieri has aerial roots.

layer, the exodermis, separates the velamen from the cortex. The exodermis consists of both thick-walled cells and passage cells that shuttle water and nutrients to the cortex of the root. An innermost layer, the endodermis, separates the cortex from the central cylinder or stele which is composed of vascular tissue, the phloem and the xylem. The phloem shuttles food, and the xylem transports water and minerals to the plant.

One of the problems of the epiphytic lifestyle is that water and nutrient supply are precarious and sporadic. Orchid roots penetrate neither into soil nor into the living tissue of their hosts. Even though they may live in an area of high rainfall, when the rain stops, they grow in a harsh, dry environment with brutally little access to moisture. Gerhard Zota and Uwe Winkler did a series of experiments showing that velamen allows the orchid to capture and retain the first solutions arriving in a rainstorm, which have the most nutrients. They found that dry velamen very quickly absorbed the water. Within 15 seconds, the velamen of 11 species tested was almost fully saturated. Within a minute, it was fully saturated. In contrast, water loss from a different set of ten species' velamen was extremely slow, taking several hours. Thicker velamen retained much more water after an hour. *Miltonia spectabilis*, with the thinnest velamen, took one hour to lose the water stored in the velamen. *Phalaenopsis* Malibu, with the thickest velamen, had lost only about fifty percent in that time. The velamen acts as a place for temporary water storage, allowing more time for absorption through the passage cells which maximizes intermittent rain fall. When the velamen dries out, empty velamen cells slow water loss. Fibrous caps found above the passage cells also restrict water loss. David H. Benzing and associates at Oberlin College suggested that differentially thickened cells below aeration points in the root may open and close, expand and contract like leaf stomata, to retain water. These adaptations help orchids be quick on the uptake and slow on the release of precious water.

The experimenters also explored the role of velamen in nutrient retention and showed that charged particles, like negatively-charged phosphate, were also retained in the velamen, probably due to positive charges in the cell walls. Another study by Martin Trepanier and associates showed that aerial roots of phalaenopsis could absorb large amounts of nitrogen from urea and ammonium directly through the velamen.

It has, in addition, been suggested that velamen may prevent overheating by reflecting heat with its white color although this needs further study.

Miltonia spectabilis var. *moreliana*

The presence of velamen is not confined to epiphytic plants, and there are numerous terrestrial orchids with velamen. Benzing, in 1996, felt that terrestrial orchids with velamen could go through repeated drying cycles without damage. A collapsed cortex can kill the root, and the velamen provides mechanical protection against desiccation, preventing collapse. There are also some orchids which lack velamen altogether.

On the other hand, velamentous roots are not unique to orchids and have also been found in other plant families such as Araceae, Liliaceae, Dioscoreaceae, Taccaceae, Amaryllidaceae, and Commelinaceae.

The Dirt on Mycorrhiza: The Root Fungus

Velamen is not the only orchid root adaptation for survival. The ability to attract and digest mycorrhizal fungi is another vital root adaptation. It allows the orchid access to extra food, nutrients, and water in a difficult environment. It is a hundred years since Noel Bernard and Hans Burgeff realized that orchids are married to fungi. The fungi that associate with orchids are called mycorrhizae. The very name itself implies a relationship between the Greek "mykos" or fungus and "riza" or roots. Mycorrhizal infection is a universal feature of the Orchidaceae.

Orchids specialize in deceiving other life forms both above and below ground. Above ground, orchids often promise pollinators food, sex, and a place to breed for their pollination services; in one-third of cases, they give nothing at all in exchange! Below ground, and sometimes above, they lure fungi into their roots and offer them the promise of a free lunch and then eat them up, giving little or nothing in return. In the give and take of life, orchids are most often the takers. Liars and cheats, orchids make a living by exploiting other species.

Ninety percent of other plant families involve fungi at some point in their life cycles, the fungus receiving carbon in sugars and the plant receiving water and nutrients. However, orchids seem to be the only large higher plant family that consistently exploits fungi as an alternative food source—effectively and one-sidedly parasitizing the fungus. (Although Cameron and associates recently showed some carbon transfer from adult *Goodyera repens* to its fungal partner, there is very little research proving that orchids do not consistently take advantage of fungi. Perhaps future research will change this view.) During some life stages, such as the germination and growth of seed, the orchid relies entirely on fungus for growth, while at other stages, the orchid makes use of both fungus and light-based nutrition, sometimes one supplementing the other. Some orchids grow entirely underground, totally dependent on fungus, like *Rhizanthella gardneri*. These orchids have to tap into the nutritional pipeline of a fungus.

Mycorrhizae are divided into ectomycorrhizal and endomycorrhizal fungi. The endomycorrhizal fungus has threads that penetrate the root cell wall and grow in intricate coils. The ectomycorrhizal fungus has threads that form a sheath on the outside of the root, a net that does not penetrate the cell wall. They are often associated with woody trees like oaks, pines, and eucalyptus and form a tripartite relationship with orchid, fungus and tree.

Fungi are not plants and cannot produce their own food through photosynthesis. For food, they break down dead organic material or attack and live on or within living plants, animals, and sometimes other fungi. It is impossible to pick up a handful of dirt and not pick up a handful of fungi. They are everywhere. There are more than one million species of fungi, at least six times more than plant species. Since they spend most of their lives underground, we are often unaware of their ubiquitous presence until we see their fruiting bodies (mushrooms or toadstools), eat shiitake mushrooms in an omelet, or develop athlete's foot at the gym. Fungi can grow to enormous sizes; in the Malheur National Forest in eastern Oregon, it was reported that a fungus *Armillaria ostoyae* (honey mushroom) extended over 2200 acres with a mass of 605 tons, thought to be the

©Adrian Davies/Minden Pictures

Fungal hyphae (mycelia)

In the Malheur National Forest in eastern Oregon, it was reported that a fungus *Armillaria ostoyae* (honey mushroom) extended over 2,200 acres with a mass of 605 tons, thought to be the largest organism in terms of area in the world.

largest organism in terms of area in the world.

The fundamental structure of a fungus is the mycelium consisting of thin, transparent, filamentous tubes called hyphae. Branching, they spread out into the soil or substrate and can grow almost indefinitely. In one cubic meter (yard) of soil, it is estimated that there can be 20,000 km (12,000 miles) of hyphal threads! About 1/60th of the thickness of a normal orchid root, they can penetrate into narrow and distant places that orchid roots cannot, shuttling back food and water for the orchid. The mycelia function as a giant root extension to feed the orchid, one end of the fungus proliferating in the orchid root and the other extending out into the soil to the food source—the great fungal food highway. Orchid roots typically are small and unimpressive, and the large fungal surface area greatly increases the volume of food and water available to the orchid.

Orchids consume fungi as a food source in a process called mycotrophy, and the orchids' amazing ability to make a living in inhospitable environments is best understood in the context of mycotrophy. Since the mycorrhiza represents an alternative source of energy, orchids can grow in deep shade. They can live without chlorophyll or leaves. They can spend years underground. For example, forty percent of the extremely rare *Isotria medeoloides* remains underground in any one year. It must survive solely from mycotrophy during that period. Most commonly, cells of the root cortex are infected to a greater or lesser by a particular group of endomycorrhizal fungi. Once within the cells, the fungus forms coiled, branching hyphal masses, intricately looped structures called pelotons, which are digested by the orchid. Reinfection then often occurs, and the process repeats, sometimes many times. It is not clear how the orchid repeatedly attracts the fungus that it digests.

Roots of northern temperate terrestrial orchids, such as in *Dactylorhiza purpurella*, show almost complete infection in the cortex soon after formation. Fungi are essential for terrestrial nutrition in a world with little open sunlight. In contrast, the root infection among tropical species is usually less dense and may be very sparse. The aerial roots of epiphytic orchids are not infected until they come in contact with a suitable substrate. Parts that remain aerial are usually not infected. Epiphytic orchids seem to be less dependent on fungi for survival than terrestrials, having more access to sunlight for food production.

However, epiphytes may still exploit fungi. Perennially threatened with desiccation and water loss, epiphytes can use fungi in their roots as a water source since fungal hyphae tips have been seen to drip with water! Living "out on a limb," epiphytes can drink fungal water exuded from the mycelia. Accompanying the transportation of water, mineral salts like phosphorus and nitrogen in the mycelium can be transported into plant tissues through the epiphytic roots. It is thought, in addition, that by digesting masses of water-rich fungal hyphae, orchid seedlings have immediate access to water before they have developed roots. Who would have thought of fungus as watering orchids?

Orchids are usually divided into classifications—terrestrial, lithophytic, or epiphytic and warm, intermediate, or cool-growing, but they could also be divided into three different classifications based on their carbon nutrition:

1. **Fully autotrophic species** (relying completely on themselves and using sunlight, CO2, and H2O to make their own food). This includes the majority of adult orchids although ongoing research may find many of these also occasionally benefit from fungi. These plants are green and have chlorophyll. As adults, they obtain carbon through photosynthesis. Nevertheless, these orchid still associate with fungi called "Rhizoctonia" that include the fungus families Ceratobasidiaceae, Sebacinaceae, and Tulasnellaceae. "Rhizoctonia" are mostly saprotrophic or parasitic.
2. **Fully mycoheterotrophic species** or **MH** (relying completely on fungi for food). World-wide there are 400 species of plants that depend entirely on fungi for their life cycle. There are at least 100 orchid species that are fully MH. They don't have chlorophyll and often spend significant time underground. They most often associate with ectomycorrhizal fungi in a three-way relationship with big plants and trees.
3. **Partially MH species** or **mixotrophic species** (relying on both sunlight and fungi). These intermediate plants combine some fungal carbon with some photosynthetic carbon, sometimes alternating or combining the two. It is suspected that this is much more common in the orchids than previously thought.

No matter what their adult nutrition, all orchids start life as seeds the size of specks of dust with no endosperm (food for the seed embryo). They all rely on fungal colonization of the seed to develop into an underground MH (fungally-dependent), achlorophyllous (no chlorophyll) stage called a protocorm. Without a fungus, absolutely no orchid seed could develop into an adult plant.

Mycoheterotrophic Species The Kids Who Never Grow Up

Some kids never leave home and never earn their own living. Some orchids are like that. They continue to be moochers their whole lives, not even bothering with chlorophyll, leaves, or photosynthesis. There are at least 100 species of orchids that never make a living through photosynthesis. They are known as fully mycoheterotrophic (MH) species, obligately (completely) dependent on fungi for the necessities of life. Transitions from being independent photosynthetic plants to being MH have occurred.

Neottia nidus-Avis, a non-photosynthetic, fully mycoheterotrophic orchid relies completely on *Rhizoctonia* fungus for nutrients. (It is called the Bird's Nest Orchid because its tangled roots look like a bird's nest.)

Tripartite Relationships

In the movie *Avatar*, all the plant life in the forest is connected. Magical underground connections link the plants and trees into an interdependent whole. In nature, something just as magical occurs with some MH orchids which form a tripartite relationship linking orchids, fungi, and trees. The sugars produced by the tree via photosynthesis are transferred to the fungi in the roots which (reluctantly) funnels it to the orchids. Ian Hood (2005) describes the unusual relationship between the leafless genus *Gastrodia*, five species of *Armillaria* fungus, and pine trees. Native *Gastrodia* such as *Gastrodia elata*, *Gta. cunninghamii*, and *Gta. sesamoides* have all become rather common in New Zealand since the planting of pine plantations. The author did a study on *Armillara* root disease in pine trees and regularly found the orchids among the root systems of young *Pinus radiata* trees infected with the fungi. Large numbers of the orchid tubers (swollen roots) were unearthed when they excavated the roots system of one infected tree. The tubers were vertically oriented 40 cm. (15 inches) below the soil surface. The fungi coated the roots of the pine trees and sucked nutrients, which they carried to the orchids. It is possible that the planting of pine plantations fostered the spread of the native orchids by enticing the fungi into the area.

The New Zealand Native Orchid Journal states that Ella Campbell (1962) identified this phenomenon 50 years ago with *Gastrodia cunninghamii* in beech forests in parts of Fiordland in New Zealand. She recognized that there was an underground connection between beech trees, *Armillaria* fungus, and the *Gastrodia*. The fungi that infect them both transport nutrients from the beech trees to the orchids. *Gastrodia cunninghamii* has also been reported beneath willow (*Salix*) trees.

Gastrodia elata is an important herb in traditional Chinese medicine and is used for everything from headache, lightheadedness, pain, and convulsions. Found in Sichuan, Yunnan, and Guizhou provinces in China, it was difficult to cultivate when natural supplies ran low. In the 1970s, scientists discovered the orchid tuber required the *Armillaria mellea* mushroom mycelium in order to grow and another fungus, *Mycena osmundicola*, in order to sprout the seeds. It is amusing to note that the medicinal effects are found mainly in the metabolites of the *Armillaria* mushroom, and you could just grow and harvest the mushroom and not bother with the orchid. Today, in China, they frequently use the mushroom and leave the wild endangered orchid alone.

The rare Australian underground orchid, *Rhizanthella gardneri*, is another orchid living in a tripartite relationship. In 1928, the farmer John Trott burned his fields and discovered some dead, buried stumps of broom honeymyrtle (*Melaleuca uncinata*). Trying to remove the stump, he discovered its association with some pale plants which had bloomed entirely underground. The botanist C.A. Gardner, for whom the orchid was named, discovered that the orchid is basically a rootless rhizome (underground stem) whose leaves are reduced to non-functioning scales. *Rhizoctonia* fungi enter through the masses of white hairs on the rhizome which may be a foot below the soil surface. Fungal threads grow from the rhizomes and surround the roots of the *Melaleuca* trees shuttling nourishment to the orchid. Totally devoid of chlorophyll, the orchid is totally dependent on this fungal pipeline. A second extremely rare Australian orchid, *Rhizanthella slateri* also a subterranean-blooming orchid, grows in eucalypt forests..

The three-way association with trees has been observed for over a century. Among the fully MH orchids, there now remains only a tiny minority that are known to obtain carbon via a fungal association with dead material. These, like *Erythrorchis altissima* (syn. *Galeola altissima*, *Erythrorchis ochobiense*), and *Cyrtosia septentrionalis* (syn. *Gla. Septentrionalis*) associate with aggressive tree pathogens and wood-decaying fungi not leaf litter or humus decay fungi.

There are interesting conservation implications in these tripartite relationships since the cutting down of forest trees may adversely affect orchids which rely on them. Often, the relationship is with old growth forest trees that are not easily replaced.

Conservation concerns make us look not just at an orchid but to the complete environment that nourishes them. The Australian MH orchid, *Dipodium hamiltonianum*, associates with *Russulaceae* fungi. These fungi are the common dietary components of marsupials in the Australian woodland, and the orchid roots are eaten threatening extinction of the orchids. On such subtle relationships depend the health of our orchids.

In the past decade, DNA analysis has shown that many MH orchids have switched from the ancestral trait of associating with rhizoctonias to form epiparasitic associations with higher basiomycetes (mushroom fungi) that are the ectomycorrhizal partners of trees and shrubs and that are not normally associated with orchids. An epiparasite is a parasite on a parasite. The fungi parasitizes the living tree by forming a net around the roots. Then the orchid digests the fungi, parasitizing the parasite! When the fungus is full of food and water from the tree, the orchids eats it!

Corallorhiza maculata photographed *in situ* in Nevada Co., CA

Corallorhiza striata

Look, Ma, No Roots!

Some MH orchids are notable for the fact that they have no roots at all! Chlorophyll-deficient *Corallorhiza* species and *Epipogium aphyllum* rely on a subterranean rhizome system and hyphae to provide enough water to produce an inflorescence. They don't bother with roots at all, being heavily and permanently infected with fungi. Some orchids like *Corallorhiza striata* have characteristic black rhizomes due to the presence of highly melanized fungi. These MH plants are densely branched with each rhizome branch being supported by a tiny scale leaf. Since the main axis is bent at the point where lateral shoots come out, it is thought to resemble coral, and the pattern is called coralloid, hence the name *Corallorhiza* or "coral root." *Epipogium* is called "The Spurred Coral Root." Coral root is, of course, a misnomer, since these are not roots at all, just long-lasting, swollen, misshapen stems. *Epipogium aphyllum* is also called "The Ghost Orchid" because although it spends most of its life underground it makes brief unexpected appearances above ground. It has a ghostly, pale, waxy appearance because it has no green pigment.

MH plants with no chlorophyll characteristically exhibit high fungal specificity, meaning that they grow only with one or a few fungal partners. *Corallorhiza striata* and its complex is high on the scale of specificity toward fungi in the genus *Tomentella*, specifically *T. fuscocinerea*. The *Corallorhiza maculata-mertensiana* species complex exhibits high specificity toward the ectomycorrhizal *Russulaceae* fungi and there is no overlap in the fungi on which they depend. This narrow range of partners seems to be the hallmark of the more than 400 fully MH plants.

This narrow range would seem to put the orchid in a very vulnerable position, but it is thought that it eliminates the challenges of attracting and defending against a wide range of associates. The orchid seems to have picked the specific fungus in the area that is the most permanent and reliable source of the highest quality nutrition. MH orchids live or die by their fungus and benefit by being choosy. It is common in nature for parasites to develop specificity toward their conquests as the two engage in a kind of arms race to capture and outsmart each other. Orchids are not only parasites but parasites on parasites (epiparasites), in this case on fungi. Completely dependent on its partner, the MH orchid will, however, switch to another fungus if necessary. For example, *Goodyera pubescens* switched from one *Tulasnella* species to another when it was drought-stressed. Non-MH orchids and seedlings seem to be much less specific in the kind of fungi they allow to infect them.

Gastrodia sesamoides photographed *in situ* near Nowra, New South Wales, Australia

Some feel that this specificity may have led to the large numbers of orchid species. In three closely related species in the MH *Hexalectris spicata* complex (all of these closely related species are now considered one species and are so listed on the World Checklist of Selected Plant Families), there was found to be association with three closely-related but distinct fungi. It has been suggested that this mycorrhizal specificity eventually led to the formation of distinct orchid species and may have driven the orchid family's amazing diversity.

The Australian species *Gastrodia sesamoides* (also naturalized in South Africa) produces no roots and lives off a rhizome that forms stem tubers. *Rhizanthella gardneri*, another bizarre Australian orchid, has a similar rhizome system that emerges only above the soil to flower. It is thought that termites pollinate this hidden marvel of nature. With a single fungal partner, it exhibits characteristic MH specificity. These completely rootless examples show to what a large extent MH orchids rely on fungi for nutrition.

Species with little chlorophyll and leaves that are ephemeral or having no leaves at all need to modify their roots in odd ways. *Galeola* species have an extensive system of long roots with branches of short mycotrophic roots. The long roots carry the lateral roots to pockets of high fungal activity. This specialization of roots also occurs in the West Indian species, *Wullschlaegelia aphylla*, which has two types of roots, some heavily infected and some not at all.

Mixotrophs—They Can but Sometimes They Just Don't Want To!

There are 17 plant families with some green members that often don't bother with photosynthesis as adults and just tap into "the underground highway" of fungal nutrition when they feel like it. Green orchids can get as much as ninety percent of their carbon from their association with fungi. Some orchids are not fussy about which fungi they rely on, and some are more specific. Marc-Andre Selosse (2004) of the National Museum of Natural History in Paris examined *Epipactis microphylla*, a green orchid that remains dependent on fungi despite the fact that it can perform photosynthesis. It can, but it just chooses not to get all its carbon from photosynthesis. Some seventy-eight percent of these orchids are colonized as adults by truffles, to the extent that foragers can use the presence of *Epipactis microphylla* to hunt for truffles! Other *Epipactis* and *Cephalanthera* species also are used to indicate truffle habitat.

Using a technique that assesses how much of the organic carbon and nitrogen found in the leaves was acquired from their fungal partners, a large number of green orchids like those in the genus *Cephalanthera*, *Epipactis*, and *Cymbidium* have carbon and nitrogen higher than the surrounding autotrophic plants but less than fully MH plants, which suggests that they are getting at least part of their carbon via photosynthesis and part through fungal partners.

Cephalanthera austinae photographed *in situ* in Humboldt Co., CA is completely heterotrophic.

Photosynthetic orchids in the tribe Neottieae obtain large amounts of their carbon from association with ectomycorrhizal fungi. *Limodorum abortivum* does not make enough food through photosynthesis and supplements its carbon supply by associating with ectomycorrhizal species. It has been thought that this mixotrophic habit was the evolutionary step that preceded the complete reliance on fungi. The shift to exploiting ectomycorrhizal fungus is thought to represent a more stable and reliable source of carbon than just relying on saprophytic fungi, which may not have a stable food supply.

The roots of orchidoid species such as *Orchis*, *Platanthera*, and *Dactylorhiza* show something called "root dimorphism" in which development is divided into fat root tubers with a special storage anatomy and also slender mycotrophic roots to provide fungal energy. They alternate between using fungal and light energy. The slender roots last less than a year, growing in the autumn or spring and dying down in the summer when leaves disappear. The tuberous roots store energy for the following year's growth, allowing the plant to survive a leafless season. The name "orchid" itself, meaning "testicle" in Greek and Latin, originates in the twin root tubers of *Orchis* species which reputedly resembled testicles to ancient orchid observers. Some-

Orchis mascula stores food in its testicular tubers.

A large clump of *Cypripedium calceolus* photographed near Jena in eastern Germany.

times the tubers are flattened and even "palmate" resembling a hand as in *Dactylorhiza*. (*Dactylorhiza* means finger roots.)

Dactylorhiza species alternate periods of green leafy growth with a season when they subsist on their tubers and root fungi. Both the roots and the tip of the tuber remain mycotrophic until spring when the new leaves emerge. Rasmussen cited the early work of Fuchs and Ziegenspeck in 1924, who found that the nitrogen content in leafless plants of *Dactylorhiza* increased by about forty-three percent during the winter months, stored carbohydrates increased by twenty-five percent and structural polysaccharides and fiber increased by eleven percent in the period during which they were totally dependent on fungi. Clearly, this is a mixotrophic orchid, using both sunlight and fungi alternatively for survival.

With *Platanthera chlorantha,* another seasonally leafless orchid, Burgeff in 1936 noted many hyphae emanating from little "rhizoids" in parts of the root where the pelotons were alive and estimated that an adult plant of *Platanthera chlorantha* had roughly 11,000 "rhizoids" which provided three times as much hyphal connection to the soil. These threads are able to rapidly proliferate in the event of local or sudden food shortage and exude enzymes to break down complex compounds in the soil, something which the orchid is not able to do. This orchid is able to switch to a largely fungal life in the event of an emergency.

Other orchids have been shown to use energy sources alternatively. A population of *Cypripedium calceolus* remained underground and unnoticed for years until the forest above it was cleared. Two years later, the orchid switched from living off its fungal root partner and emerged above ground, switching to photosynthesis for its food. Nobody had even known that the orchid was there before this flowering.

J.D.W. Dearnley and associates (2012) make the additional claim that many more species will be found to be mixotrophic:

> The habitat of many epiphytic species that live in the shade of the dense forest canopy is typified by low irradiance, and it is possible that species will soon be identified as mixotrophic with a dependence on external-supplied carbon as well as photosynthesis.

Trash Basket Roots

An interesting variation on root growth is the de-

Coryanthes mastersiana

Coryanthes panamensis has trash basket roots that provide a home to ants.

velopment of so-called "trash basket" roots. Some orchids, such as *Ansellia africana*, *Coryanthes macrantha* and *Grammatophyllum speciosum*, quickly develop an extensive, entangled root system of erect roots at their base. This spectacular matrix of roots collects leaf litter and debris, nourishing the orchid. In some of the plants with trash basket roots, extrafloral nectar is also secreted on new shoots, bracts, and outer surface of the orchid buds, attracting ants that nest in the roots. The ants collect vertebrate feces to fertilize the orchid and aggressively defend their nest. The ant gardens grow epiphytically or lithophytically and consist of masses of soil, detritus, and chewed plant parts, all assembled at the branches of the trees. All orchids in these partnerships are highly adapted, mostly obligate (only existing in one environment) ant-garden plants.

Coryanthes is a genus that grows exclusively in these so-called "ant gardens" living in orchid roots. These ant/orchid root balls can grow five feet in diameter (150 cm) with the ant nest itself comprising 31 inches (80 cm). Both organisms share a common destiny because the *Coryanthes* is thought to die if the associated ant colony dies. Ants offer defense against herbivores and debris nutrition, and the orchid offers a root framework for nest construction and extrafloral nectar. Nutrition that the ants provides allows the plant to grow more rapidly. Flowering in only two-to-three years from seed, an orchid record, *Coryanthes* produce massive flowers, each weighing more than three ounces (100 g), the most massive individual flowers in the orchid family. Capsules containing 600,000 seeds mature rapidly in only two months. Many other genera in their subtribe take more than six months for the seed capsule to mature and produce seeds.

Often trees have more than one *Coryanthes* ant garden. In Guatopo National Park in Venezuela, Günter Gerlach found a mango tree with more than ten *Coryanthes* ant gardens. Ants often live in polygynous (more than one functioning queen in a colony) colonies or have extensions of their primary colony and are thought to carry seeds from a capsule opening in their ant-garden to their extension colonies.

David Jeffrey et al. (1970) stated that many orchid genera have species with roots occupied by ants—*Gongora, Grammatophyllum, Vanda, Cattleya, Dendrobium, Coelogyne, Vanilla, Arundina, Oncidium,* and *Spathoglottis*.

Root Structure

Roots have four major functions—absorption of water and nutrients, storage of food, prevention of soil erosion and attachment to a substrate. Orchids, have a root system formed by "adventitious" roots. Adventitious roots, from the Latin *adventicius*, meaning "not belonging to," are roots that form on organs other than a central root (such as a taproot) but usually form from the stem of the plant. Monopodial orchids (leaves arise from the same, indeterminate, apical meristem. Rhizomes and pseudobulbs are absent) such as phalaenopsis often have aerial roots that are produced at intervals along the main stem and grow out into the air. Some attach for support, some go down into the pot, and many are pendent. The active roots are white with brown or green tips while growing. Sympodial orchids develop multiple growth shoots successively from the axillary buds of a horizontal stem called a rhizome. Roots of sympodial orchids grow from the rhizome. They are white, fleshy and have a spongy covering. The growing tips are green, reddish brown, or olive. In both monopodial and sympodial orchids, the growing tip of the root is pushed forward by the division of cells immediately behind it. Colored root tips contain pigments to protect chloroplasts from excessive light.

There is not just one type of orchid root. Spanning the globe and living in many different microsites, orchid roots can be very different. Some are fleshy and thick as in *Vanda tricolor,* and some are fibrous and thin like *Acianthera pubescens* (syn. *Pleurothallis smithiana*). Some are branched, and some are not. Some are aerial, like phalaenopsis roots, and others grow upward to form a nest or trash basket like *Coryanthes*. Some burrow into the forest floor like paphiopedilum roots or hang from wet rock faces like those of phragmipediums. Terrestrial orchid root anatomy can be different from epiphytic root anatomy, and temperate orchid roots can differ from tropical orchid roots. Most species have cylindrical roots, although some are dorsiventral in structure, flattened with a top and bottom surface. The oddest of these are the green flattened roots of leafless orchids which have replaced leaves as the major photosynthetic organs like *Dendrophylax lindenii*, the Ghost Orchid.

Terrestrial orchids have an anatomy not much different from the roots of tulips, lilies or hyacinths. There is a protective outer layer of epidermal cells. Each cell has an external cell wall made up mainly of cellulose fibers. Sometimes these may also contain some lignin (the compound that makes wood) or suberin (the compound that comprises cork). The wall gives structure and some protection from drying out. In certain orchids like *Goodyera hachijoensis* or *Cephalanthera longifolia*, epidermal cells have long protrusions called root hairs that help with water and mineral uptake. Inside the epidermal layer is the cortex that serves as a storage area. The cortical cells can contain starch grains, mucilage or calcium oxalate raphides (needle-shaped crystals). The innermost layer of the cortex, the endodermis, borders the central stele (the central cylinder) which contains phloem and xylem systems. Xylem is the vascular tissue that conducts water and mineral salts from the roots to the leaves, and phloem is the vascular tissue of a plant through which metabolites are transported.

Fungal infection of the roots of terrestrial orchids is common. Generally, the infected plants have thick, sparsely branched roots, and the uninfected have a very simple system of only a few, usually unbranched roots that are typically fleshy, thick, and brittle. They are often contractile. Usually, there is only one stele, but more than one have been found in the roots of several *Platanthera* species.

The roots of epiphytic (growing on tree branches) and lithophytic (growing on rocks) are similar because in both cases the roots are exposed to air and light. They are photosynthetic, perennial, and fairly constant throughout the year. Roots of terrestrial orchids, on the other hand, are usually non-photosynthetic, live less than three years and often show seasonal differences in growth and composition. In addition, they are usually buried in soil or leaf litter unlike the aerial roots of epiphytes. Moreover, to stay alive, terrestrial orchids are much more dependent on fungus living in their roots than epiphytic orchids.

It has been noted that tropical orchids have thicker velamen layers than temperate orchids. Tropical orchids

The 'Ghost Orchid,' *Dendrophylax lindenii* 'Tiny Jungle' AM/AOS.

tend to be attached to bark as epiphytes and benefit from thick velamen in that dry environment. A tropical orchid such as *Catasetum fimbriatum* or *Stanhopea lietzei* can have up to 15 velamen cell layers. Temperate orchids are terrestrial and live in humus, which provides and retains moisture and nutrients, and they generally don't require thick velamen. To further prove this, Johansson in 1974 discovered in the Nimba Mountains of Liberia that orchids growing in insignificant amounts of wet humus, such as species of *Aerangis*, *Plectrelminthus*, and *Rangaeris*, developed a thick velamen.

A diversity of fungi have been found to be associated with orchids, mostly isolated from orchid roots. They have also been found to be in protocorms (tuber-shaped bodies with roots that are the first seedling stage of an orchid) and occasionally in rhizomes (a plant stem that grows horizontally under or along the ground and gives rise to an upright shoot). The fungi most commonly include a heterogeneous assemblage of mycelia referred to as the genus *Rhizoctonia*, but this is not a single species or genus. The mycelia lack sexual sporulation (producing spores) and are identified solely on the basis of their hyphal (thread like structure which is very fine and colorless that makes up the body of the fungus) characteristics.. Orchids have even been associated with such gourmet fungus as truffles and shiitakes.

Catasetum fimbriatum has fifteen layers in its thick velamen.

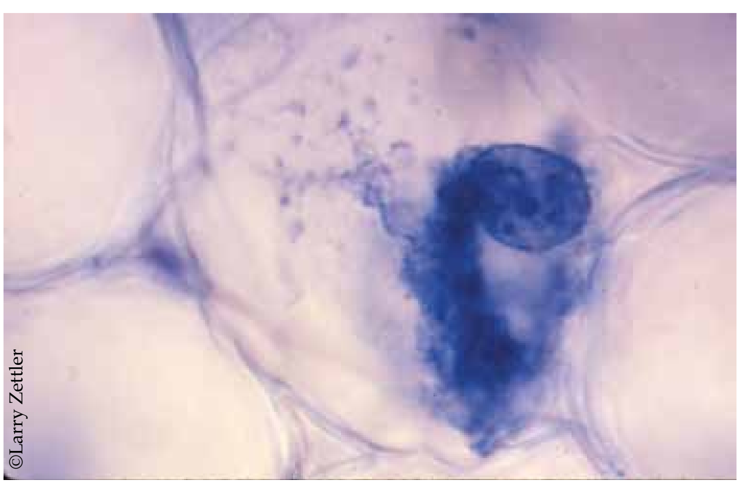
Epipactis palustris

Fungi are most often found in areas of the cortex below epidermal hairs, especially close to the root tip. When infected, the root tends to becomes fairly yellowish or opaque of the root. All protocorms are infected with fungi, but after roots are formed on the new seedling, there is a greater chance that the new roots will be colonized by a secondary soil infection which would often be unsuitable for germinating the seeds. The first roots most often develop before aboveground leaves. Starch is often stored in the new roots, but disappears after the cells have become infected with fungus.

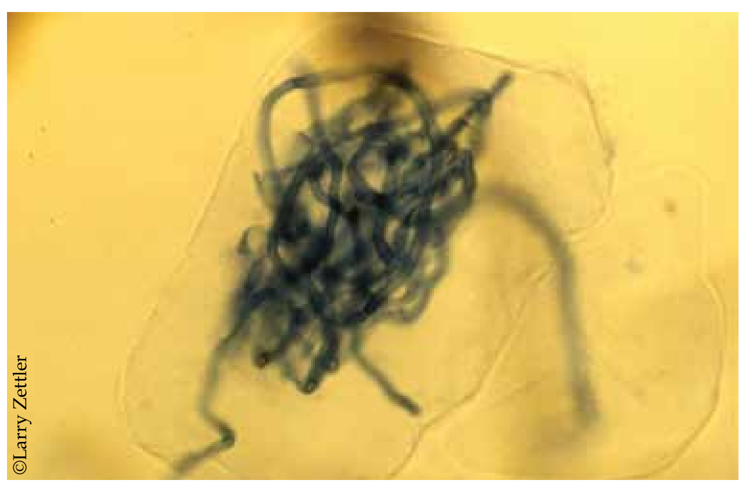
Interestingly, most plant roots other than orchids have more xylem (water transport) than phloem (metabolite transport) in the stele. Hanne Rasmussen reported that water transport is not the main concern in infected orchid roots, and there is a preponderance of phloem. Rasmussen pointed out that it seems that the carrying of water is antagonistic to mycotrophy. A major part of the stele is required to be phloem to transport the nutrients from the digestion of pelotons (an undifferentiated bundle of fungal hyphae found inside a plant cell in an endomycorrhizal association). Once pelotons are digested, more xylem often returns to carry water, at least until new infection re-emerges.

Mycotrophic roots of orchids, with their alternative food source, seem nutritionally to be independent of the rest of the plant. The fascinating consequence of this is that detached root fragments, remaining alive in the soil for a long time, can even give rise to new plants.

Roots sometimes grow in strange directions. Terrestrial roots often grow horizontally or even upwards. *Dactylorhiza majalis*, *Dact. incarnata*, *Gymnadenia conopsea*, and *Gym. nigra* roots grow upward toward the leaf litter or into the humus, the area which supposedly has the most fungi. *Epipactis palustris* has some horizontal roots that penetrate humus layers as well as vertical

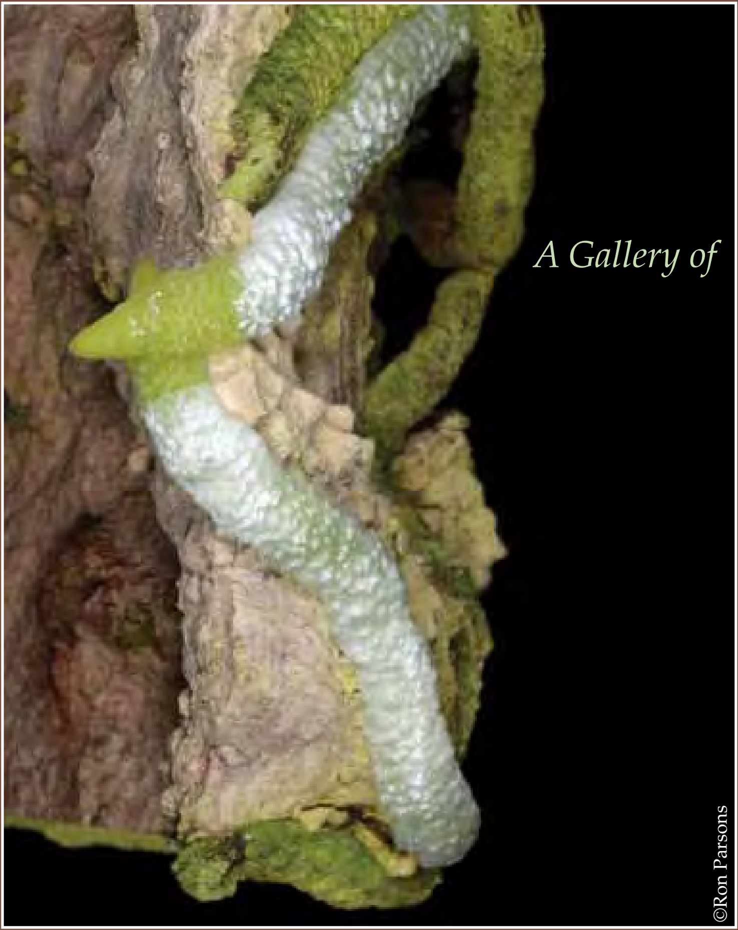


Peloton digested by *Platanthera integrilabia.*

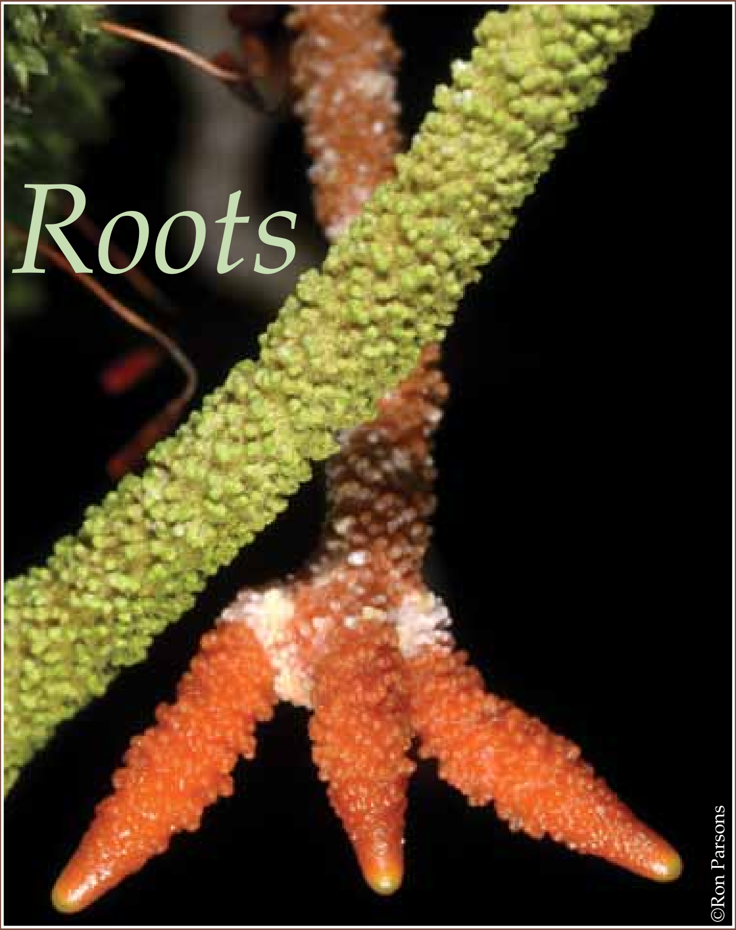


Enlargement of peloton in *Platanthera integrilabia.*

A Gallery of Roots



Angraecum dryadum has verrucose root that are silky in texture.



The orange-tipped roots of *Angraecum viguieri* are papillose.

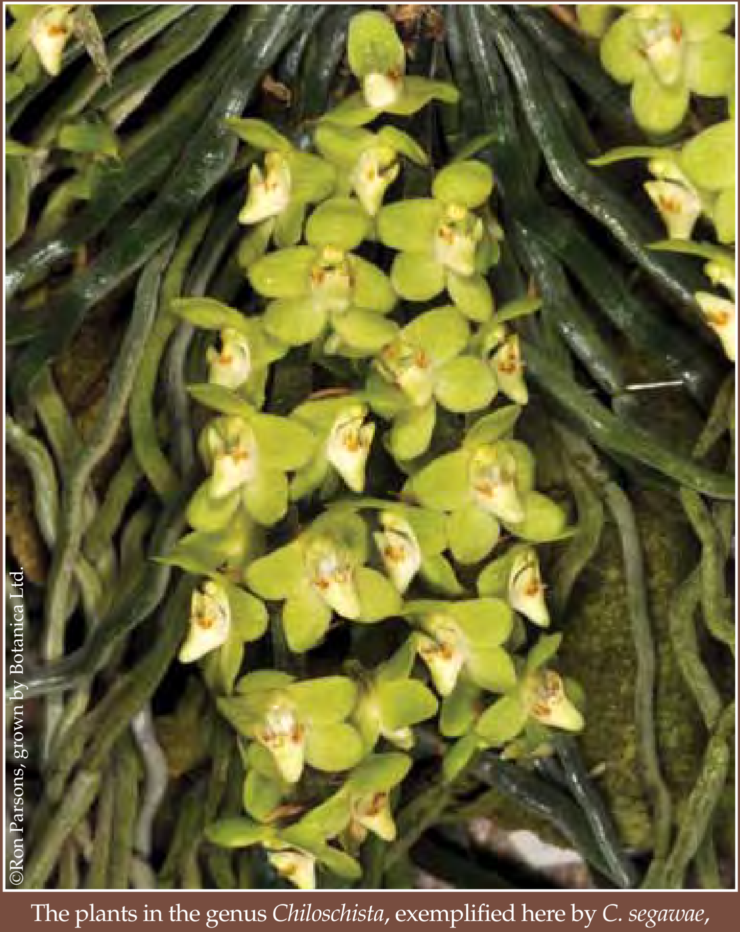
Typical of many species in the genus, *Bulbophyllum macranthum* produces a flush of roots on the new growth.

The green-tipped roots of *Dendrobium aurantiflammeum* are numerous and fine.

The smallish canes of *Dendrobium dichaeoides* bear aerial roots.

The smooth roots of various *Trichoceros* species are proportionally large.

Microcoelia species are all leafless. Here is *Microcoelia stolzii* 'Cathy Fenwick's Medusa' CHM/AOS.



The plants in the genus *Chiloschista*, exemplified here by *C. segawae*, consist of nothing more than roots and a few, quickly-deciduous leaves.

roots that grow deep into the soil.

With ingenious adaptations for water and mineral retention and with the exploitation of fungi and ants, orchids have truly found a very effective way to survive. In a difficult world, orchids have evolved magnificent roots that make life possible in challenging environments and difficult conditions.✾

Acknowledgements

I am most grateful to Harold Koopowitz and Alec Pridgeon for reviewing my manuscript. Many thanks to Ron Parsons, my most generous friend and supporter, for his many beautiful images that he took specifically for this article. Thanks to Dr. Joseph Arditti for permission to use Wendy Zomlefer's drawing of root anatomy. Gratitude also to Larry Zettler for the generous use of his fungi images.

References

Arditti, Joseph. *Fundamentals of Orchid Biology.* New York: John Wiley and Sons. 1992.

Attenborough, David. *The Private Life of Plants.* Princeton: Princeton University Press. 1995.

Baluska, Frantisek, Stefano Mancuso, Dieter Volkmann and Peter W. Barlow. "The 'Root-brain Hypothesis of Charles and Francis Darwin: Revival After More than 125 Years," *Plant Signalling and Behavior*, 4 (12) December 2009: 1121-1127.

Barret, Craig F., John V. Freudenstein, D. Lee Taylor and Urmas Koljalg. "Rangewide Analysis of Fungal Association in the Fully Mycoheterotrophic Corallorhiza striata Complex (Orchidaceae) Reveals Extreme Specificity on Ectomycorrhical Tomentella Across North America," *American Journal of Botany*, 97 (4) April 2010: 628-642.

Cameron, Duncan D., Irene Johnson, David J. Read and Jonathan R. Leake. "Giving and Receiving: Measuring the Carbon Cost of Mycorrhizas in the Green Orchid, Goodyera Repens," *New Phytologist*, 180 2009:176-184.

Dearnaley, John. "Further Advances in Orchid Mycorrhizal Research," *Mycorrhiza* , 17 (6) 2007: 475-486.

Dearnaley, J.D.W., F. Martos, and M.A. Selosse. "Orchid Mycorrhizas: Molecular Ecology, Physiology, Evolution and Conservation Aspects," in *Fungal Associations 2nd edition The Mycota IX*. Berlin: Springer-Verlag. 2012.

Hadley, G. and B. Williamson. "Features of Mycorrhizal Infection in Some Malayan Orchids," *New Phytology,* 1972:1111-1118.

Hadley, Geoffrey. *Orchid Mycorrhiza in Orchid Biology Review and Perspectives II* Edited by Jospeph Arditti: 83-118. Ithaca and London: Cornell Press, 1982.

Jeffrey, David C., Joseph Arditti and Harold Koopowitz, "Sugar Content in Floral and Extrafloral Exudates of Orchids: Pollination, Mymecology and Chemotaxonomy Implications,"*New Phytology*, 69 1970: 187-195.

Keel, Brian G. "Shifting Distributions: The Orchid-Fungal-Climate Change Connection," *Orchids*, 8 (1) January 2011: 48-51.

Leake, Jonathan R. "Plants Parasitic on Fungi: Unearthing the Fungi in Myco-Heterotrophs And Debunking the Saprophytic Plant Myth," *Mycologist*, 19 (3) August 2005: 113-121.

Oliviera, Virginia del Carmem and Maria das Gracas Sajoe. "Root Anatomy of Nine Orchidaceae Species," *Brazilian Archives of Biology and Technology*, 42 (4) 1999: 207-230.

Pandey, Madhav, Jyotsna Sharma, Donald Lee Taylor and Vern L. Yadon. "A Narrowly Endemic Photosynthetic Orchid is Non-Specific in Its Mycorrhizal Associations," *Molecular Ecology*, 22 2013: 2341-2343.

Pennis, Elizabeth. "The Secret Life of Fungi," *Science*, 304 June 2004: 1620-1622.

Pridgeon, Alec. *The Velamen and Exodermis of Orchid Roots in Orchid Biology Review and Perspectives IV.* Edited by Joseph Arditti: 1987 139-192.

Rasmussen, Hanne N. *Terrestrial Orchids: From Seed to Mycotrophic Plant.* Cambridge: Cambridge University Press. 1995.

Selosse, M.A., A. Faccio, G. Scappaticci, P. Bonfante. Chlorphyllous and Achlorophyllous Specimens of *Epicactis microphylla* (Neottieae, Orchidaceae) are Associated with Ectomycorrhizal Septomycetes, including Truffles. *Microb Ecol,* 47 2004: 416-426.

Siegel, Carol. "Orchids and *Formicidae*: Ants in Your Plants." *Orchid Digest,* 78 (3) July Aug Sept 2014: 150-161.

Stephenson, Steven L. *The Kingdom Fungi: The Biology of Mushrooms, Molds and Lichens.* Portland: Timber Press. 2010.

Trepanier, Martin, Marie-Pierre Lamy and Blanche Dansereau. "Phalaenopsis Can Absorb Urea Directly Through Their Roots," *Plant Soil*, 319 2000: 95-100.

Warcup, J.H. "The Mycorrhizal Relationships of Australian Orchids," *New Phytologist*, 87 1981: 371-381.

Waterman, Richard J. and Martin I. Bidartondo. "Deception Above, Deception Below: Linking Pollination and Mycorrhizal Biology of Orchids," *Journal of Experimental Botany*, 59 (5) March 2008: 1085-1096.

Yoder, Jay A., Lawrence W. Zettler, and Scott L. Stewart. "Water Requirements of Terrestrial and Epiphytic Orchid Seeds and Seedlings and Evidence for Water Uptake By Means of Mycotrophy," *Plant Science*, 156 2000: 145-150.

Zettler, Lawrence W. "Nature's Fungal Connoisseurs: New Insights into the Mysterious Orchid- Fungal Association, *Orchids*, 74 (4) April 2005: 292-297.

Zotz, Gerhard and Uwe Winkler. "Aerial Roots of Epiphytic Orchid: The Velamen Radicum and Its Role in Water and Nutrient Uptake," *Oecologia*, 141 2013:733-741.

http://en.wikipedia.org/wiki/Mycorrhiza, accessed 5/20/2014.

http://www.aos.org/images/img_content/

newsletter_issues/oct09.html, "Beginner's Newsletter," accessed 5/25/2014.
http://www.nativeorchids.co.nz/Journals/89/Newsandviews.htm accessed 4/20/2014.
http://www.nativeorchids.co.nz/Journals/89/Page5.htm. Ian St George. "Getting Close and then Cheating," accessed 4/20/2014.
http://www.nativeorchids.co.nz/Journals/94/page19.htm Ian Hood "Armillaria and Gastrodia in Pine Forests," February 2005, accessed 4/20/2014.

About the Author

Carol Siegel, a retired English teacher and medical office manager, has been president and newsletter editor of the Greater Las Vegas Orchid Society for several years. She lectures on many subjects at societies, museums, and universities around the country and has written articles on Nevada's native orchids in addition to many for the *Orchid Digest*. Carol leads groups of Clark County school children on tours of the Springs Preserve, a museum and nature center complex.

Carol Siegel
E-mail: growlove@cox.net