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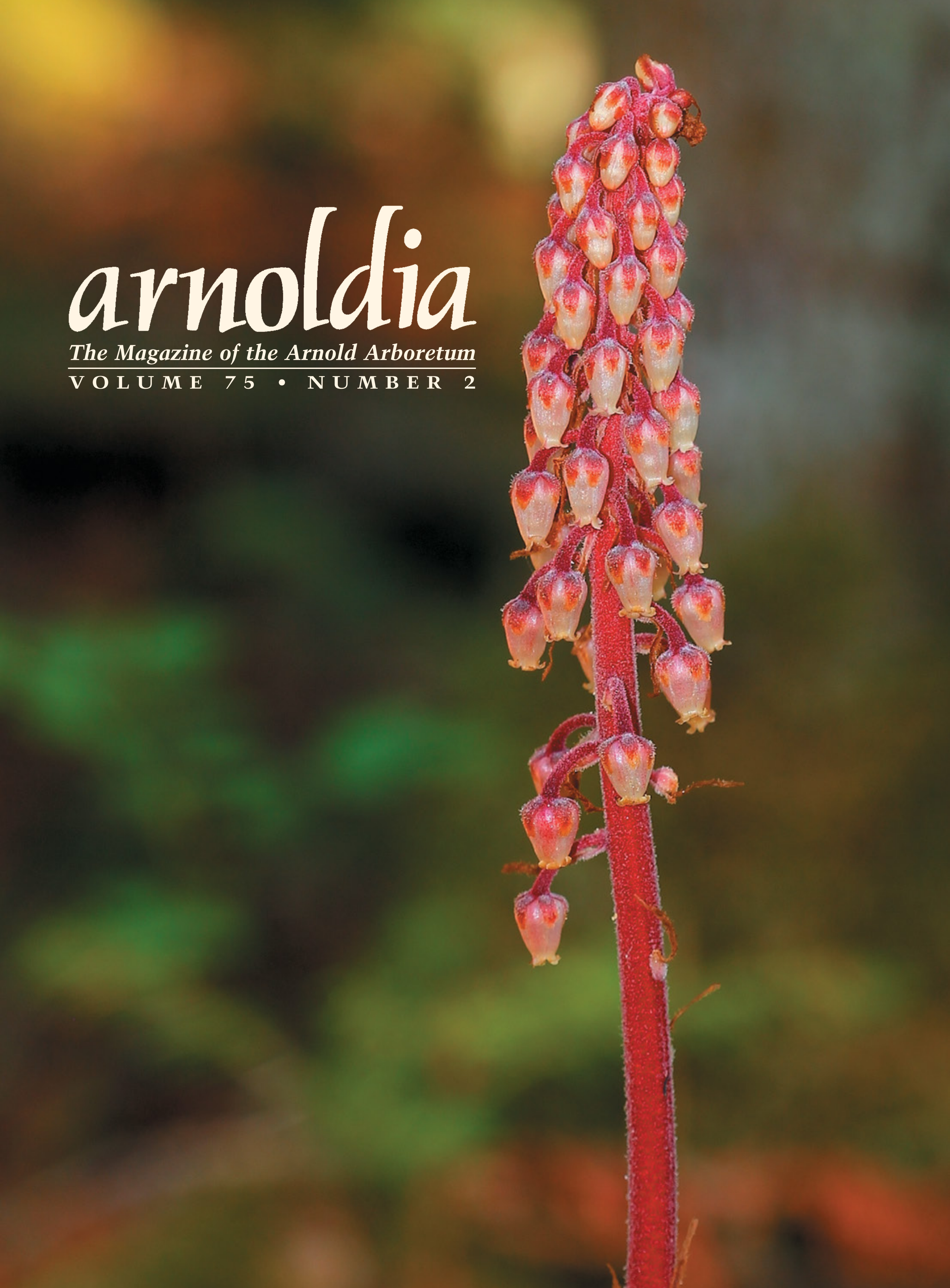
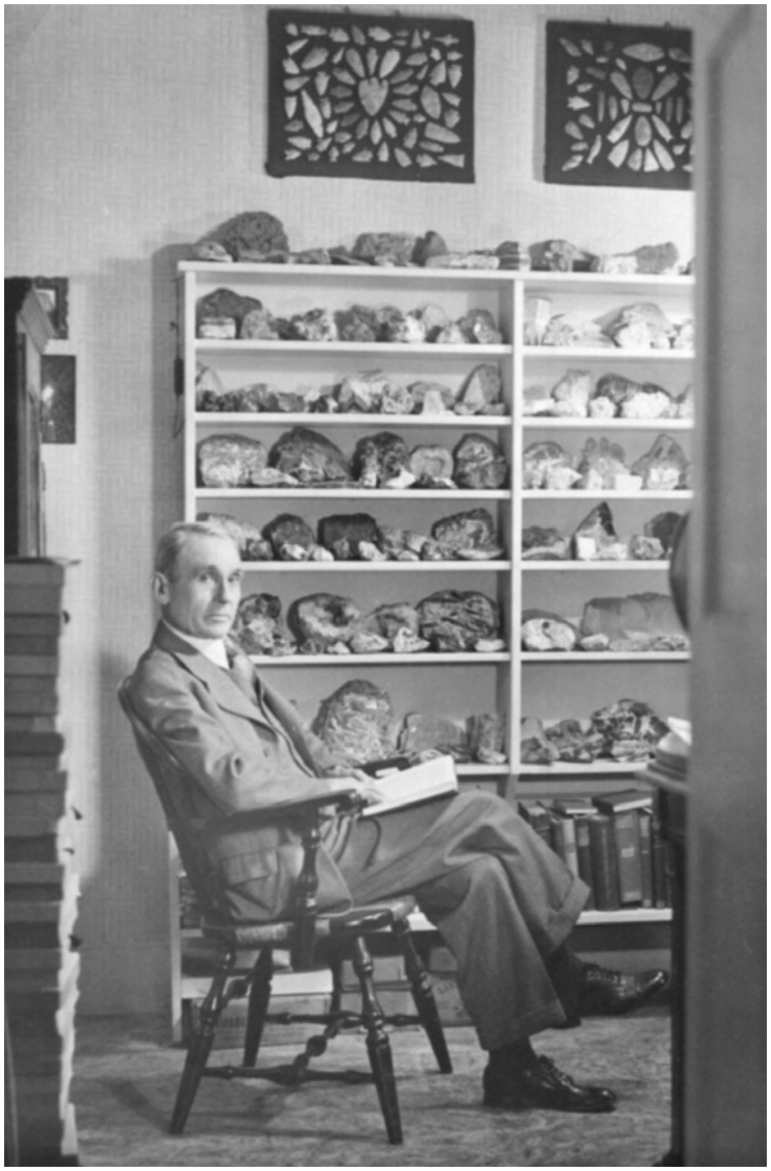
The Magazine of the Arnold Arboretum

VOLUME 75 • NUMBER 2





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Front cover: Woodland pinedrops (*Pterospora andromedea*) is a mycoheterotroph, a non-photosynthetic plant that acquires carbohydrates from photosynthetic plants by connecting to mycorrhizal networks. Photo by Rob Routledge, Sault College, bugwood.org

Inside front cover: Botanist and plant collector Ernest Jesse Palmer had a long relationship with Charles Sprague Sargent and the Arnold Arboretum. He is seen here, circa 1947, in his study in the house at 1090 Centre Street with just part of his extensive collection of minerals, fossils, and artifacts on display. Photo courtesy of Theodore W. Palmer.

Inside back cover: Unlike most members of its genus, Bunge ash (*Fraxinus bungeana*) bears showy, fringe-like flowers (upper photo). A striking variegated Bunge ash seedling was discovered at the Morris Arboretum and has been given the cultivar name 'Sunflash' (lower photo). Photos by Kang Wang (upper) and Anthony S. Aiello (lower).

Back cover: Autumn color develops in a red maple leaf (*Acer rubrum* 'Schlesingeri', accession 408-91-A). Photo by Nancy Rose.

Food, Poison, and Espionage: Mycorrhizal Networks in Action

David Yih

Can trees nurse their young? Do plants send out signals underground to warn each other of the arrival of ravenous insects? Can they go on the attack themselves and cripple competing plants with noxious chemicals they deliver through fungal connections? Lately, researchers investigating subterranean fungal networks have come up with surprising answers to questions like these. Their intriguing findings also have game-changing implications for ecology and conservation, forestry and agriculture—even evolutionary theory.

ROB ROUTLEDGE, SAULT COLLEGE, BUGWOOD.ORG

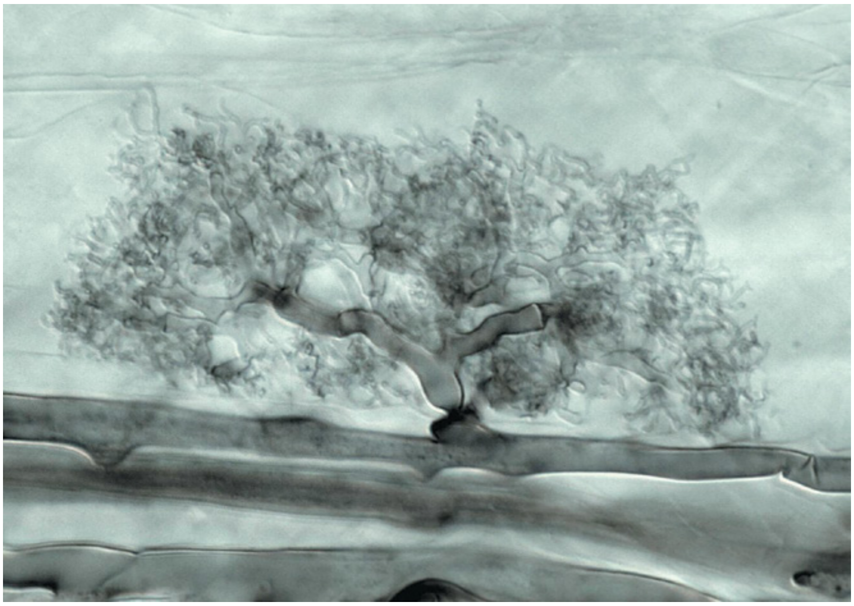
The native North American orchid, hooded coralroot (*Corallorhiza striata*), is a mycoheterotroph that relies on mycorrhizal networks for its survival.

Some 90% of terrestrial plant species around the world engage in symbioses called mycorrhizae—from Greek *mykos* (fungus) and *rhiza* (root). Mycorrhizal plants come from all corners of the plant kingdom and include trees, forbs, grasses, ferns, clubmosses, and liverworts. Their symbiotic partners (symbionts) are fungi whose threadlike hyphae radiate out into the soil, bringing water and nutrients—including phosphorus, nitrogen, zinc, and copper—back to the plant's roots in exchange for a share of the carbohydrates plants produce through photosynthesis. Though mycorrhizal symbioses range along a continuum from parasitic (on the part of the plant) to mutualistic types, most are mutually beneficial. By themselves, plants can only access nutrients in the immediate vicinity of their feeder roots, and soon exhaust the supply. By associating with fungi, they conserve resources that would have been spent on growing ever larger root systems. In fact, as Smith and Read state categorically in their compendium of all things mycorrhizal, "Mycorrhizas, not roots, are the chief organs of nutrient uptake by land plants" (Smith and Read 2008).

Subway Lines

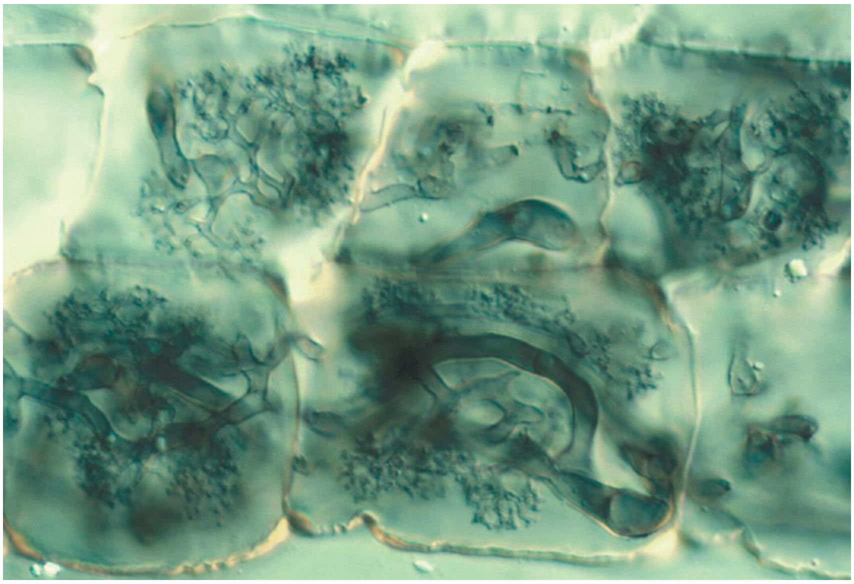
When compatible mycorrhizal fungi and plants recognize each other and create an interface in the plants' roots for the exchange of nutrients, they can form a variety of structures in and around the roots, depending on the species involved. Broadly speaking, there are two main types: arbuscular mycorrhizae and ectomycorrhizae.

Arbuscular mycorrhizae get their name from the classic shape that the fungi take inside root cells, a profusely branching form called an arbuscule. As its name suggests, an arbuscule has a miniscule tree- or shrub-like shape. The creation of an arbuscular mycorrhiza begins when chemicals exuded by a plant's roots stimulate a nearby arbuscular mycorrhizal fungus to branch and grow, allowing it to quickly find the roots. Once in contact, the fungus adheres to the root surface and, within a few days, penetrates the root and begins the formation of a mycorrhiza.



MARK BRUNDRETT

This tree-shaped arbuscule within a plant cell is part of an arbuscular mycorrhizal fungus in the genus *Glomus*.



MARK BRUNDRETT

Both coils and small arbuscules can be seen within these root cells of yellow trout lily (*Erythronium americanum*).

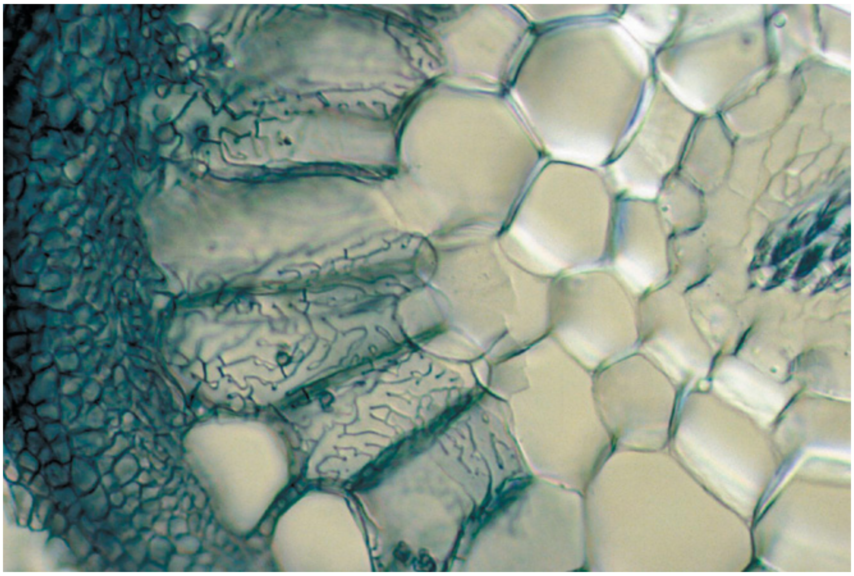
Inside the root, different arbuscular mycorrhizal structures may develop, depending on the particular species involved. In 1905, the botanist Ernest-Isidore Gallaud named arbuscular mycorrhizal structures after plant genera he found them in. *Arum*-type mycorrhizae resemble maps of bus or subway lines: hyphae grow into the space between rows of cells, extending alongside them, like avenues running past city blocks, and making "stops" along the way to enter cells and form arbuscules. Though it penetrates a root cell's wall, the fungus remains in what amounts to an antechamber; it never passes through the cell's plasma membrane. Instead, this membrane envelops the invading hypha and all of its branches, maximizing the area of mutual contact. At this interface, plant and fungus establish a sort of marketplace where each partner deposits nutrients and trades them for nutrients deposited by the other.

Gallaud named the other main form of arbuscular mycorrhiza the *Paris* type, after a Eurasian plant genus (a relative of *Trillium*). In the *Paris* type, the fungus forms coils that look like chaotic loops of strewn intestines. An occasional small arbuscule may branch off from a coil, but the *Paris*-type mycorrhiza lacks a straight "subway line" traveling alongside the cells. Instead, a coiling hypha exits from one cell only to enter the adjacent one, where it forms another mass of coils before moving on to the next cell—definitely not the express train!

Arbuscular mycorrhizae have been around for a long time. Researchers have found arbuscules in fossils of *Aglaophyton,* an extinct genus of pre-vascular plant, dating from around 410 million years ago, in the Devonian Period. In fact, most scientists agree that the first plants to colonize the land were symbiotic organisms containing structures very similar to arbuscular mycorrhizae (Smith and Read 2008). Given their lengthy tenure on the planet, it's not surprising that arbuscular mycorrhizae occur in nearly all species of herbaceous plants and in most trees and shrubs. But the other main mycorrhizal type—the ectomycorrhiza (going back a mere 50 million years)—is also extremely important. While only about 3% of seed plants are ectomycorrhizal, they occupy large expanses of the earth's terrestrial surface. Almost all are woody plants, and they include forest trees that are the world's main sources of timber, such as pines. Starting alphabetically, *Abies, Acer, Alnus, Betula, Carpinus,* and *Corylus* are a few of the eastern North American genera containing at least one ectomycorrhizal species.

ROBERT L. ANDERSON, USDA FOREST SERVICE, BUGWOOD.ORG

Ectomycorrhizal roots of a container-grown conifer.



MARK BRUNDRETT

The Hartig net of an ectomycorrhizal fungus extends among poplar (*Populus*) root cells.

Ectomycorrhizae differ from arbuscular mycorrhizae in several other ways. Unlike arbuscular mycorrhizal fungi, ectomycorrhizal fungi mostly do not penetrate root cells, hence their designation as "ecto-" meaning "outer" or "external." The hallmarks of an ectomycorrhiza are the fungal sheath, which encloses the root tip in a dense mass of hyphae, and the Hartig net, a labyrinthine hyphal network that grows between the outer layers of the root's cells. Another difference involves the relative numbers of associated fungus species. Despite the vast numbers of arbuscular mycorrhizal plant species, their fungal symbionts consist of only about 150 species, all in the division Glomeromycota. Inversely, a more diverse group of about 5,000 to 6,000 fungus species form ectomycorrhizal associations. And while all arbuscular mycorrhizal fungi are microscopic and subterranean, many ectomycorrhizal fungi develop large fruiting bodies that occur either above or below ground. Those that appear above ground include many common woodland mushrooms, while the most notable of the underground-fruiting ectomycorrhizal fungi belong to the genus *Tuber,* best known for its fruiting bodies, truffles.

Sharing Food

We can visualize a mycorrhiza as a simple one-to-one relationship between an individual plant and an individual fungus. But in nature the picture is more complex. As the threadlike hypha of a mycorrhizal fungus extends outward from a plant's roots, it frequently encounters the roots of other plants of the same or different species. It may form mycorrhizae with these new partners, while still maintaining its connection with the first plant. As it proliferates in new directions, the hypha branches and fuses repeatedly, weaving a fungal net through the surrounding soil. Meanwhile, additional fungi of the same or different species may approach the first plant. If they're compatible, the plant is apt to form mycorrhizae with them, too. Soon a diverse association appears, composed of various fungi and various plant species, big and small, all connected into a sizeable mycorrhizal network that may span hundreds of hectares of forest (Gorzelak et al. 2015). The promiscuous nature of these associations of multiple plant and fungus species has prompted scientists to give their papers playful titles like: "Changing partners in the dark," "Mycorrhizal networks: *des liaisons dangereuses,*" and "Architecture of the wood-wide web."

Mycorrhizal networks are highly efficient at procuring essential plant nutrients from the soil while the plant partner provides the carbon that fungi require. But the carbon doesn't stop there. It's long been known that certain nonphotosynthetic, parasitic plants, called mycoheterotrophs, depend on carbon shuttled from photosynthesizing plants via mycorrhizal fungi (see next page). The seeds of most mycoheterotrophs are tiny "dust seeds," consisting of only a few cells and little or no endosperm to supply the germinating plant with food. Thus, these species depend upon mycorrhizal fungi for their survival. The orchids, perhaps the largest family in the plant kingdom, depend entirely on carbon received via mycorrhizal fungi for successful seed germination and early development. Experiments have shown that certain green orchids can convey carbon back to their associated fungi once they reach maturity. Thus, they partake in mutualisms that are offset in time, like borrowers repaying a loan. But "full mycoheterotrophs" (including some orchids) depend, throughout their lives, on carbon received through mycorrhizal networks, apparently without benefit to the fungus.

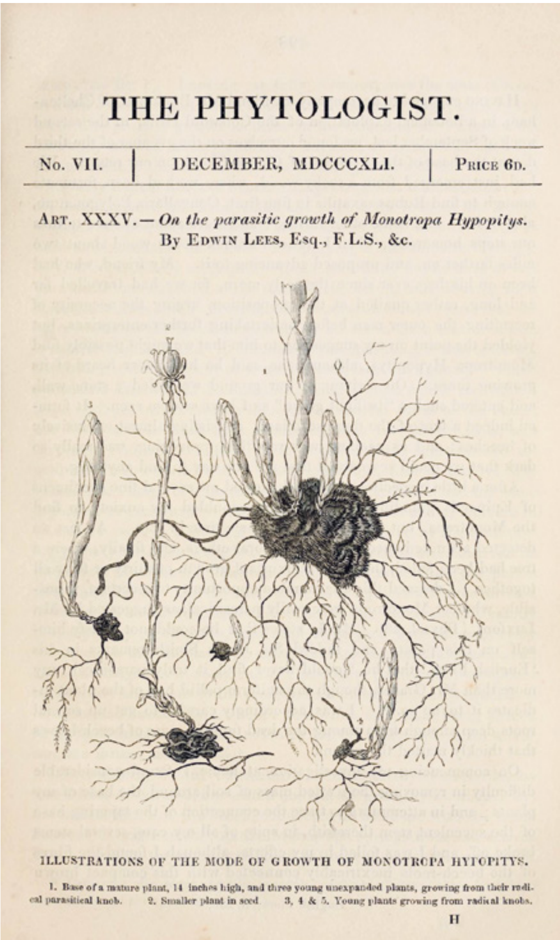
In recent years investigators have discovered that mycorrhizal networks can distribute resources in much more flexible ways than previously thought, sending them in the direction of greatest need in response to changing conditions, in a seasonal tide-like flux. Researchers at Laval University in Quebec found evidence that carbon moved via mycorrhizal networks from yellow trout lilies (*Erythronium americanum*) to young sugar maples (*Acer saccharum*) as the maples' leaves unfurled in spring, and then back to the trout lilies in the fall during rapid trout lily root growth (Lerat et al. 2002). The direction of carbon flow can reverse even more frequently. University of British Columbia researchers reported that the flow of carbon changed direction not once but twice in the course of a growing season. In the spring, carbon traveled from Douglas-fir (*Pseudotsuga menziesii*) to paper birch (*Betula papyrifera*) as its buds resumed growth. In the summer, carbon flowed from heavily photosynthesizing paper birch into stressed Douglas-fir in the understory. And in the fall, it flowed from still-photosynthesizing Douglas-fir into paper birch as it shed its leaves (Simard et al. 2012).

Other resources besides carbon can change direction too. Though water typically flows from mycorrhizal fungi into the roots of their plant symbionts, under extreme conditions it can go the other way. In a greenhouse experiment, investigators using dye tracers found that when soil became extremely dry, oaks that were able to access water through their deep taproots transferred water to their mycorrhizal fungi, thus keeping them alive (Querejeta et al. 2003). Plants can even defend their fungal partners from fungivores. A recent study found evidence that when springtails (tiny insect-like

Mycoheterotrophs and the Birth of Mycorrhizology

The first impetus for the investigations that culminated in the discovery of mycorrhizae in the nineteenth century came from a puzzling group of plants that grew in the gloom of the forest floor. The ghostly apparitions lacked chlorophyll and had only vestigial leaves. Instead of spreading deeply into the soil, their roots tended to be tangles of truncated "coralloid" stubs. How did such plants thrive in the darkness?

In 1841, when a British entomologist and botanist named Edward Newman decided to publish a new monthly called *The Phytologist,* he had no idea that a controversy would arise among its pages that would mark the beginning of an entirely new field of inquiry. At the center of the debate was a peculiar plant that Linnaeus had named *Monotropa hypopitys* (now *Hypopitys monotropa,* yellow pinesap). With a wide distribution encompassing much of temperate Eurasia and North America, pinesap was one of the most common achlorophyllous plants in Britain, and its odd lack of green color cried out for an explanation. As early as 1821, William Jackson Hooker had posed the question of whether the plant was a parasite. Botanists had long been aware of the existence of parasitic plants, like those in the genus *Orobanche,* that attached themselves to other plants' roots. But the nature of pinesap's attachment, if any, to other plants' roots was unclear. In 1840, the Austrian botanist Franz Unger had looked at the closely intertwined roots of pinesap and Norway spruce (*Picea abies*) and concluded that it was not a parasite. A year later, the editor of *The Phytologist* proposed to its readers that they take up the question. The first response, from Edwin Lees, appeared in the December 1841 issue: the plant was a parasite on beech roots. Two issues later, another contributor came to the opposite conclusion: the plant *was not* a parasite. Soon more readers joined the fray, and the controversy raged on for months. The one thing the respondents could agree on was that they'd all seen an annoying profusion of mysterious fibers that impeded their attempts to observe any connection between tree roots and pinesap roots.



THE PHYTOLOGIST.

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ART. XXXV.—*On the parasitic growth of Monotropa Hypopitys.* By EDWIN LEES, Esq., F.L.S., &c.

ILLUSTRATIONS OF THE MODE OF GROWTH OF MONOTROPA HYPOPITYS.

1. Base of a mature plant, 14 inches high, and three young unexpanded plants, growing from their radical parasitical knob. 2. Smaller plant in seed. 3, 4 & 5. Young plants growing from radical knobs.

H

The status of pinesap remained an open question until 1960, when Swedish investigator Erik Björkman used the carbon-14 isotope to trace the movement of carbon into pinesap from nearby trees. Lees had actually hit the mark when he'd written that the strange fibers looked fungal and appeared to be "imbibing nutriment from the rootlets of beech to which they are closely applied, and conveying it to the succulent radicles of the Monotropa, with which they are also connected." Pinesap turned out to be a previously unknown type of parasite that acquires carbohydrates from green plants by connecting to mycorrhizal networks. Scientists have dubbed such plants *mycoheterotrophs* and speculate that they evolved from photosynthetic mycorrhizal plants adapting to the darkness of the forest floor. Having no requirement for sunlight, most full mycoheterotrophs are subterranean for much of their lives. Some even flower and set seed underground!

hexapods) browse on mycorrhizal fungi, plants can help by sending protective chemicals into the hyphae (Duhamel et al. 2013).

What about the extraordinary idea that plants might be subsidizing their progeny—essentially nursing them—using mycorrhizal networks? Though there is no clear evidence that plants can detect their kin through mycorrhizal networks and shuttle nutrients preferentially to offspring, there are hints in that direction. Ferns reproduce in a life cycle that passes through two distinct generations. Spores from the familiar, leafy sporophyte generation germinate and grow into the tiny, rarely seen gametophyte generation, which, through sexual reproduction, gives rise to the next generation of sporophytes. Researchers working with two species of the fern genus *Botrychium* found that strains of *Glomus* (a genus of arbuscular mycorrhizal fungi) maintained mycorrhizae with individuals of both generation types simultaneously, demonstrating the potential for sporophytes to subsidize the achlorophyllous gametophytes (Winther and Friedman 2007). Since then, a number of studies have shown that tree seedlings do indeed benefit from resources received from mature trees of the same species via mycorrhizal networks, though not necessarily to a greater degree than other plants in the network.


JOSEPH O'BRIEN, USDA FOREST SERVICE, BUGWOOD.ORG

THOMAS G. BARNES, UNIVERSITY OF KENTUCKY

Research showed that mycorrhizal networks reversed the movement of carbon between yellow trout lilies (*Erythronium americanum*) and sugar maples (*Acer saccharum*) during the year.

Notes from the Underground

The hustle and bustle of mycorrhizal networks becomes even more intriguing as we look beyond resource sharing to the remarkable communication functions of mycorrhizal networks. What do plants need to talk about? Like many animal species, plants have a language of danger. In the early 1980s, David Rhoades, a zoologist interested in the interactions between insect herbivores and plants, proposed a novel idea. In the course of his research with *Salix sitchensis,* he had noticed that defensive changes in the leaf chemistry of willows being chewed on by tent caterpillars also showed up in the leaves of nearby plants, even though they had not yet been attacked. He speculated that the neighboring plants must have detected airborne molecules emanating from either the attacked plants or the tent caterpillars, prompting them to deploy protective chemicals preemptively (Rhoades 1983). Subsequent research confirmed Rhoades' suspicion—plants being attacked by herbivores can release volatile organic compounds into the air that induce defensive responses in nearby plants. And recent experiments have shown that such "stress signals" can also be transmitted through mycorrhizal networks. Researchers at South China Agricultural University inoculated tomato plants with the fungal pathogen *Alternaria solani,* the cause of early blight disease in tomatoes and potatoes, and became the first to demonstrate that mycorrhizal networks can act as plant-to-plant communication conduits. They found that the uninfected tomato plants (stress-signal receivers) in the mycorrhizal network showed an increase in disease resistance and putative defense-related enzyme activity. They also found that the receiver plants had activated several defense genes. These changes in the receiver plants began within 18 hours of inoculating the donor plants (Song et al. 2010).

In 2013, a group of scientists working in the United Kingdom decided to follow up on the fungal pathogen study and see what would happen with insect herbivores. They produced the first experimental evidence that signal molecules from plants infested with aphids travel through mycorrhizal networks to uninfested neighboring plants. Within 24 hours of the arrival of pea aphids (*Acyrthosiphon pisum*) on broad bean plants (*Vicia faba*), signals traveling through mycorrhizal networks caused uninfested broad beans to give off volatile compounds. Not only did these compounds repel the aphids, they actually attracted the aphids' natural enemy, the parasitoid wasp *Aphidius ervi* (Babikova et al. 2013). This interaction apparently benefits all three parties to the network. Being quickly alerted to the threat allows the uninfested beans to deploy their protective volatiles preemptively, thus evading aphid attack. The fungi thereby avoid a potentially catastrophic reduction in the plants' capacity to supply them with carbon. And even the infested beans may benefit: some investigators suggest that stress-signal transmission ensures that signal-donor plants will become engulfed in a large plume of protective volatiles created collectively by the surrounding plants in the network (Barto et al. 2012).

In some cases, attacks on plants can simultaneously stimulate both stress signals and nutrient transfers. A recent collaboration between Chinese and Canadian researchers investigated the flow of carbon and stress signals in a mycorrhizal network involving a four-month-old interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), a ponderosa pine (*Pinus ponderosae*), and the ectomycorrhizal fungus, *Wilcoxina rehmii.* They found that manual defoliation of the young Douglas-fir resulted in a transfer of both defense signals and carbon via mycorrhizal network to the ponderosa pine (Song et al. 2015). Some mycorrhizologists ascribe this result to the fungus throwing in its lot with the healthy pine rather than throwing good money after bad by propping up the struggling Douglas-fir. Postulating that the transfers were initiated by the fungus, they write: "Here, the networking fungus may have acted to protect its net carbon source, by allocating carbon and signals to the healthy, more reliable ponderosa pine" (Gorzelak et al. 2015).

Weapons of Plant Destruction

Besides tranferring resources and signals, mycorrhizal networks can extend the reach of the allelochemicals that certain plants produce—toxic substances that inhibit the development of nearby competitors. Thus, "mycorrhizal networks can serve as couriers for biochemical warfare" (Gorzelak et al. 2015). A study of the effect of mycorrhizal networks in the transport of the allelochemical juglone, which is exuded by the roots of *Juglans* species (walnuts) and negatively affects the growth of many plants including rhododendrons, tomatoes, and apples, unequivocally implicated mycorrhizal networks in the dispersal of juglone into the soil (Achatz et al. 2014).

In at least one case, instead of helping to spread noxious allelochemicals, mycorrhizal fungi themselves become the victims. Garlic mustard (*Alliaria petiolata*), a European plant well known as an invasive in eastern North America, is a non-mycorrhizal plant that produces fungicidal allelochemicals. Researchers found that garlic mustard drastically reduced the abil-

JOSEPH BERGER, BUGWOOD.ORG

Mycorrhizal networks can transmit warning signals to surrounding plants when pests such as these pea aphids attack.

ADOLF AND OLUNA CESKA

The fruiting bodies of the ectomycorrhizal fungus *Wilcoxina rehmii*.

ity of North American arbuscular mycorrhizal fungal spores to germinate and form mycorrhizae. As a result, American mycorrhizal plants had reduced seed-germination and increased mortality, while non-mycorrhizal plants were unaffected. European arbuscular mycorrhizal fungi and plants were also relatively unaffected, presumably due to their long evolutionary exposure to garlic mustard's allelochemicals (Callaway et al. 2008).

Another peculiar relationship between invasives and mycorrhizal networks involves spotted knapweed (*Centaurea stoebe,* formerly *C. maculosa*), which is invasive in many areas and covers over seven million acres in the United States. It's of particular concern in the West, where Idaho fescue (*Festuca idahoensis*) is a common native grass. University of Montana researchers estimated that as much as 15% of the above-ground carbon in spotted knapweed plants came from nearby fescue by way of mycorrhizal fungi (Carey et al. 2004). Thus, invasives may exploit mycorrhizal networks to thrive at the expense of neighboring native plants.

Networking for the Future

Understanding mycorrhizal networks is evidently important for effective conservation of many species. This is particularly true of mycoheterotrophs, which cannot survive apart from mycorrhizal networks. According to Martin Bidartondo of the Royal Botanic Gardens at Kew, "myco-heterotrophic plants are excellent indicators of undisturbed forests and forests with old-growth characteristics" (Bidartondo 2005). It follows that mycoheterotrophs are among the species at greatest risk of extirpation from the clearcutting of forest lands (Moola and Vasseur 2004). Mycoheterotrophs are extremely host-specific, so their conservation must involve both their particular fungal host species and the green plants that supply carbohydrates as essential habitat components.

With the increased resistance to diseases and pests and the better access to water and nutrients that mycorrhizal networks offer, there is increasing recognition of the potential for a new "Green Revolution" based on using mycorrhizae in crop fields and forests. Much of the world's agriculture depends upon fertilizer derived from mined rock phosphate, a non-renewable resource that is steadily dwindling. Phosphorus is a crucial plant nutrient that mycorrhizal fungi are particularly good at locating in ordinary soil and funneling back to their plant symbionts. We can lessen our dependence on rock phosphate by finding ways to work with mycorrhizae. Proposed techniques include sowing fallow fields with appropriate mycorrhizal plants to maintain the level of fungal inoculum in the soil between crop rotations, using tilling patterns that minimize disturbance of mycorrhizal fungi, and avoiding the indiscriminate use of fungicides in the soil. Many tree nurseries are finding that inoculating tree seedlings with appropriate mycorrhizal fungi increases survival both in the nursery and after planting out.

In perusing the reports mentioned in this article, I was struck by the various ways investigators conceptualized what they saw happening in mycorrhizal networks. There are large gaps in what is understood about how mycorrhizae operate, and scientists must often use human metaphors as stand-ins to bridge the gaps. One implicit question that kept surfacing was: Who were the doers of the actions taking place in mycorrhizal networks, and what were their "motives"? Were plants "nursing" their progeny to keep their species going, or were fungi redistributing resources to the young plants with an eye to their own future wellbeing? Were Douglas-firs helping paper birches so as to later receive reciprocal benefits in their hour of need, or were fungi orchestrating the flux of resources, minimizing their risk by diversifying across multiple partner species? Were stress-signal donors "warning" receiver plants, or were the receivers "eavesdropping" on donors, on the alert for potential trouble? Or were mycorrhizal fungi acting like savvy farmers, apportioning fertilizer and coordinating pest management to maximize long-term yield? Perhaps the answer is "all of the above," because ultimately all the organisms involved tend to strengthen and perpetuate their mutually beneficial networks. Indeed, when all the participants' roles are considered, the network as a whole emerges as a kind of higher-order organism in its own right, fitter than the sum of its parts, a well-ordered social entity capable of surviving the death of any of its individual members.

Some scientists argue that the groupings of species involved in mycorrhizal networks are examples of natural selection at the level of the group (Gorzelak et al. 2015). For others, the interesting question is: which is the true driver of evolution—competition or cooperation? The ground-breaking evolutionary theorist Lynn Margulis passionately insisted on the predominant role of symbiosis in evolution. And for evolutionary biologist and author Frank Ryan, the discovery of mycorrhizae was a missed opportunity. He wrote, "The intimate cooperation between wholly different life forms—plants and fungi—is not only an amazing biological phenomenon but also a vitally important factor in the diversity of plant life on earth. It should have been of enormous interest to evolutionary theorists,


NANCY ROSE

Garlic mustard (*Alliaria petiolata*) not only crowds out woodland natives but also exudes allelochemicals that negatively affect arbuscular mycorrhizal fungi.


EDWARD L. BARNARD, FL DEPT OF AGRICULTURE AND CONSUMER SERVICES, BUGWOOD.ORG

The ectomycorrhizal fungus *Pisolithus tinctorius* readily makes associations with a number of woody plants and is used in plant nurseries to improve seedling growth. Seen here, a young fruiting body (left) and associated mycorrhizal roots on slash pine (*Pinus elliottii*) seedlings.

but … at the end of the nineteenth century, as the fundamental principles of biology were being hammered into place in laboratories around the world, Darwinian evolution took center stage. And as Darwinism, with its emphasis on competitive struggle, thrived, [mutualistic] symbiosis, its cooperative alter ego, languished in the shadows, derided or dismissed as a novelty" (Ryan 2002). Perhaps its time is still to come. In the meantime, plants and their mycorrhizal networks offer a fascinating and fruitful field of inquiry on many different levels.

References

Achatz, M., E. K. Morris, F. Müller, M. Hilker, and M. C. Rillig. 2014. Soil hypha-mediated movement of allelochemicals: arbuscular mycorrhizae extend the bioactive zone of juglone. *Functional Ecology* 28: 1020–1029.

Babikova, Z., L. Gilbert, T. J. A. Bruce, M. Birkett, J. C. Caulfield, C. Woodcock, J. A. Pickett, D. Johnson, and N. van Dam. 2013. Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecology Letters* 16: 835–843.

Barto, E. K., J. D. Weidenhamer, D. Cipollini, and M. C. Rillig. 2012. Fungal superhighways: Do common mycorrhizal networks enhance below ground communication? *Trends in Plant Science* 17: 633–637.

Bidartondo, M. I. 2005. The evolutionary ecology of mycoheterotrophy. *New Phytologist* 167: 335–352.

Callaway, R. M., D. Cipollini, K. Barto, G. C. Thelen, S. G. Hallett, D. Prati, K. Stinson, and J. Klironomos. 2008. Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology* 89: 1043–1055.

Carey, E. V., M. J. Marler, and R. M. Callaway. 2004. Mycorrhizae transfer carbon from a native grass to an invasive weed: evidence from stable isotopes and physiology. *Plant Ecology* 172: 133–141.

Duhamel, M., R. Pel, A. Ooms, H. Bücking, J. Jansa, J. Ellers, N. M. van Straalen, T. Wouda, P. Vandenkoornhuyse, and E. T. Kiers. 2013. Do fungivores trigger the transfer of protective metabolites from host plants to arbuscular mycorrhizal hyphae? *Ecology* 94: 2019–2029.

Gorzelak, M. A., A. K. Asay, B. J. Pickles, and S. W. Simard. 2015. Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants* 7.

Lerat, S., R. Gauci, J. G. Catford, H. Vierheilig, Y. Piché, and L. Lapointe. 2002. C14 transfer between the spring ephemeral *Erythronium americanum* and sugar maple saplings via arbuscular mycorrhizal fungi in natural stands. *Oecologia* 132: 181–187.

Moola, F. M. and L. Vasseur. 2004. Recovery of late-seral vascular plants in a chronosequence of post-clearcut forest stands in coastal Nova Scotia, Canada. *Plant Ecology* 172: 183–197.

Querejeta, J. F., L.M. Egerton-Warburton, and M.F. Allen. 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia* 134: 55–64.

Rhoades, D. F. 1983. Responses of alder and willow to attack by tent caterpillars and webworms: evidence for pheromonal sensitivity of willows. In: *Plant Resistance to Insects: Based on a symposium sponsored by the ACS Division of Pesticide Chemistry at the 183rd Meeting of the American Chemical Society, Las Vegas, Nevada, March 28–April 2, 1982,* ed. Paul Hedin. ACS Symposium Series number 208. pp. 55–68. American Chemical Society.

Ryan, F. 2002. *Darwin's Blind Spot: Evolution Beyond Natural Selection.* Boston: Houghton Mifflin Harcourt.

Simard, S. W., K. J. Beiler, M. A. Bingham, J. R. Deslippe, L. J. Philip, and F. P. Teste. 2012. Mycorrhizal networks: mechanisms, ecology and modelling. *Fungal Biology Reviews* 26: 39–60.

Smith, S. E. and D. J. Read. 2008. *Mycorrhizal Symbiosis,* third edition. Cambridge, Massachusetts: Academic Press.

Song, Y. Y., R. S. Zeng, J. F. Xu, J. Li , X. Shen, and W. G. Yihdego. 2010. Interplant communication of tomato plants through underground common mycorrhizal networks. PLoS ONE 5(10): e13324.

Song, Y. Y., S. W. Simard, A. Carroll, W. W. Mohn, and R. S. Zeng. 2015. Defoliation of interior Douglas-fir elicits carbon transfer and stress signalling to ponderosa pine neighbors through ectomycorrhizal networks. *Scientific Reports* 5, Article no. 8495.

Winther, J. L. and W. E. Friedman. 2007. Arbuscular mycorrhizal symbionts in *Botrychium* (Ophioglossaceae). *American Journal of Botany* 94: 1248–1255.

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Ernest Jesse Palmer and Charles Sprague Sargent: A Serendipitous Relationship

Theodore W. Palmer

Ernest Jesse Palmer (1875–1962) was a highly accomplished plant collector, botanical taxonomist, and naturalist. He was employed by the Arnold Arboretum from 1913 to 1948 and, during the latter part of his tenure, lived with his family in the old farm house on Centre Street (near the Arboretum's current greenhouses). In this article, Palmer's son, Theodore W. Palmer, explains the unlikely circumstances that made this exceptional career possible.

Ernest Jesse Palmer was born in England but came to the United States when he was three years old, his family first settling in west central Missouri. From early childhood Palmer had a strong interest in natural history, an interest that was encouraged by his parents who were surprisingly well informed on many subjects although they had no significant formal education. However, when his father lost the ability to work in his midfifties, Palmer's free time and chances for his own formal education were severely restricted as he became the main source of support for his family at the age of eleven. After the family moved in 1891 to the lead and zinc mining boom town of Webb City, in southwestern Missouri, he concentrated his natural history interest on the Carboniferous age marine fossils which were abundant in the mine tailing piles.

Charles Sprague Sargent (1841–1927), founding director of the Arnold Arboretum, was the person mainly responsible for directing Palmer's career to botany. Palmer and Sargent first became aware of each other through the botanist Benjamin Franklin Bush (1858–1937). Bush had started collecting plants for Sargent and the Arnold Arboretum around 1899, after several years of doing the same for the Missouri Botanical Garden. In his obituary of Bush, Palmer wrote that in 1900 he read Bush's 1894 paper:

> In the introduction the author requested that teachers, horticulturists, or anyone interested in the woody plants of the state, send specimens to him for identification, for the purpose of bringing about a better knowledge of the flora of the state and of the distribution of the trees and shrubs. Finding many plants unknown to me, I decided to take advantage of this opportunity, and mailed a small package of twigs and leaves to him.

Bush identified botanical specimens for Palmer over several months, and arranged to visit the next year in April. He stayed with the Palmers for nearly a week and left a supply of driers for the crude plant press Palmer had constructed. After that, Bush visited Palmer repeatedly in Webb City.

Palmer sent his first specimens, some hawthorn (*Crataegus*) fruits, to Sargent in November 1901. His first attempt at shipment failed, however, as Sargent wrote to say that "many of the paper packages inside the bag broke open in transit so that the fruit was mixed. In future the fruit should be put in separate cloth bags." No doubt numbers of inept people sent such packages to the Arboretum. But Palmer corrected the matter with a second box of specimens and received the following praise from Sargent:

> I have your letter of the 18th and also your box of specimens. These are excellent and you have been very successful in drying them, for *Crataegus* is one of the most difficult of all genera to handle for the herbarium.
>
> I hope you realize how greatly I am indebted to you for your assistance in this investigation. When the spring opens I

COURTESY OF THE AUTHOR

Ernest Jesse Palmer (behind horse) in 1895, ready to deliver groceries with a horse-drawn wagon, one of many jobs he worked as a way of supporting his family.

COURTESY OF PRAIRIE MOON NURSERY

Bush's poppy mallow (*Callirhoe bushii*), a herbaceous perennial native to Missouri, Kansas, Arkansas, and Oklahoma, was named in honor of botanist Benjamin Franklin Bush.

ARNOLD ARBORETUM ARCHIVES

Charles Sprague Sargent in the Arboretum collections, photographed in 1907.

HARVARD UNIVERSITY HERBARIA

In his book *Trees and Shrubs: Illustrations of new and little known ligneous plants* (Volume 2, page 67), Sargent notes that he had botanized with Palmer near Webb City on October 2, 1901, finding the type specimen of *Crataegus aspera* (now known as *C. pruinosa*). Seen here is one of the specimens of *C. aspera* collected by Sargent that day.

BIODIVERSITY HERITAGE LIBRARY, MISSOURI BOTANICAL GARDEN

A drawing of *Crataegus palmeri* (now known as *C. reverchonii* var. *palmeri*) from Sargent's *Trees and Shrubs: illustrations of new or little known ligneous plants,* Plate 29.

> hope that you will be full of enthusiasm and ready for a new campaign, for the field about Webb City is by no means exhausted yet. I shall write you later just what it is desirable to look after in the spring. (November 22, 1901)

By 1903, Sargent had published three new species from Palmer's herbarium specimens: *Crataegus palmeri, C. lanuginosa,* and *C. speciosa,* naming the first for Palmer in *Trees and Shrubs,* Volume I, p. 57, where he wrote:

> This handsome tree of the Crus-galli Group, one of the largest and most symmetrical of American Thorns, is named for its discover, Mr. E. J. Palmer, of Webb City, who has carefully collected and studied *Crataegus* in southwestern Missouri, where the genus is represented by a large number of interesting forms, of which several are still undescribed.

Perhaps Palmer's early success was not particularly remarkable—*Crataegus* in southwest Missouri was widespread and varied. On the other hand, Palmer was able rather soon to distinguish the interesting from the commonplace, and therein lies the genius of any good collector.

Thus began a correspondence that was eventually to change Palmer's life profoundly. During the next several years, until 1907, the letters were sporadic. These were the years during which Palmer was building his taxonomic skills as well as pursuing his many other interests in natural history—all while also supporting his family with multiple jobs, starting with delivering heavy loads with his father's horse and wagon in his teenage years to being chief bookkeeper for a local oil company.

It is obvious that Sargent valued Palmer's work on his favorite subject, *Crataegus.* Palmer was eager to please all his correspondents as can be seen in his correspondence with the many small-time collectors with whom he exchanged specimens. He did no less for this great man who showed an interest in him. He worked to master *Crataegus* as well as anyone could. By 1908 one of his more colorful acquaintances, the Reverend John Davis of Hannibal, Missouri, wrote, "Mr. Bush says you know the several species [of *Crataegus*] now almost by heart; can sight them afar off, and call them all by name." Thus

COURTESY OF THE AUTHOR

The Palmer's house in Webb City, Missouri, which was designed and built by hand from scrap lumber in the mid-1890s by E. J. Palmer and his father. Palmer's sister and mother are on the front porch.

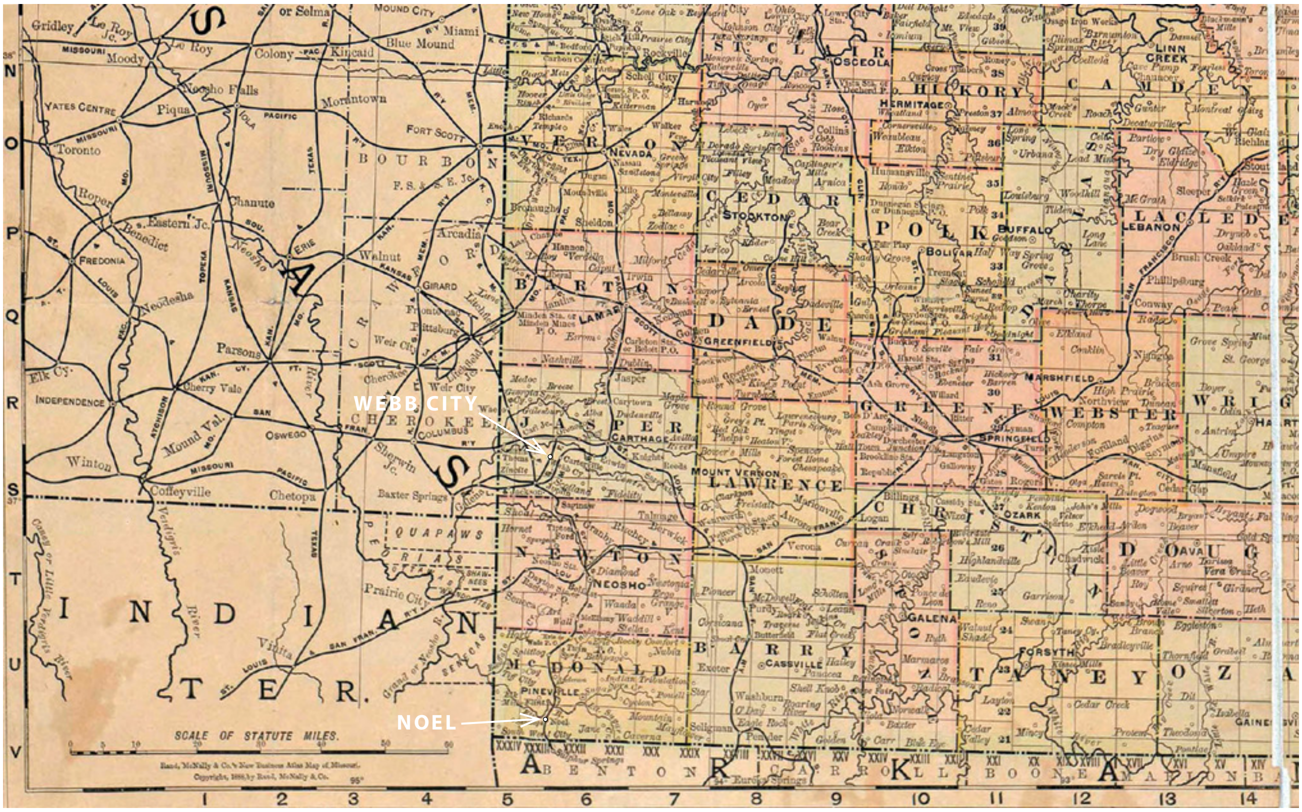
Palmer had at this early date achieved a local reputation with this confusing genus. Is it, then, surprising that Sargent wanted to hire Palmer to collect for him? On March 25, 1907, Sargent wrote:

> I now enclose a list of the *Crataegus* material collected by you or me in your region which has not yet been described. Much of it is incomplete and I very much hope that you may be able to do more work this year on these numbers.
>
> Won't you kindly write me what the prospect is and whether there is any chance of your extending your work beyond the immediate neighborhood of Webb City and Carthage? Eureka Springs in Arkansas is evidently a good field as we collected flowers there a good many years ago but have never had any fruit. Joplin, I take to be a rich field and unexplored; indeed I fancy there is no place in southwestern Missouri that you could visit without finding new forms.

But Palmer's answer was negative at this time because of his need to support his family. Sargent visited Webb City in the autumn of 1907 and stayed in the Palmer family home, as noted Dutch botanist Hugo de Vries had done in 1904. (The family, who lived in impecunious circumstances, took pride in these visits.) On the visit itself, there is no information. Palmer was then 32 years old, knew his area well, and no doubt Sargent saw a fair sampling of the surrounding countryside.

Early in 1908 Sargent again wrote asking Palmer to collect professionally:

> I have been very much impressed with the carefulness with which you have made collections and observations of *Crataegus* and your grasp of the genus. I wish you could devote more time to collecting and studying the southern Missouri. Would it be possible for you to make an arrangement with your employers by which you could get off a month in the spring and a month or six weeks in the autumn for this purpose?



THE STATE HISTORICAL SOCIETY OF MISSOURI

A Rand-McNally map, circa 1888, of southwestern Missouri; note the many railway lines, but no roads, that are shown.

> If this could be done I should be very glad to pay you the salary you now get and, of course, all your expenses. Will you think this over and let me know if it is not possible to make some such arrangement? I should like to think that the Arboretum could employ you continuously for a year or two, at least, in this sort of work, and I was rather in hopes that Professor Trelease [of the Missouri Botanical Garden] would join me in such a scheme but he does not see his way clear to doing so, and single-handed I do not see how we can manage it.... (February 18, 1908)

Again Palmer felt unable to do so; he wrote that he couldn't keep his position (as accountant with the Waters-Pierce Oil Company) and still take off so much time.

A Growing Partnership

By 1910 the relationship between the two men was such that Sargent could ask Palmer to collect very specific specimens, although Palmer would have to go to some trouble to do so. For example, on January 14, 1910, Sargent wrote:

> I believe you know that curious Hickory which grows at Noel and for which Bush suggested the name of *subvillosa.* It is one of the minima set but has smooth bark and very broad leaflets. If you know where to find the trees, would it be possible for you to run down to Noel now and get us some winter branchlets showing winter buds, etc.

Noel is nearly fifty miles from Webb City and this was before automobiles were common. There was the train, of course. Palmer said in later years that he could not have collected so widely had not the railway and electric railway afforded access to places some distance from Webb City. By this means he could go to the towns of Alba, Joplin, Duenweg, Carthage, and Galena. (In 1918 the line was extended to include Baxter Springs and Pitcher.) The fare was twenty cents round trip to anywhere

NANCY ROSE

In 1902, near Webb City, Missouri, E. J. Palmer collected the seeds from which this cockspur hawthorn (*Crataegus crus-galli,* accession 12079-A, photo from October 2017) was grown.

within a fifty mile radius, and Palmer would take his bicycle along to give him mobility once he reached his destination. In the case under discussion, Palmer did secure the hickory specimen. He would, throughout the remaining years as a collector, go far out of his way to obtain a desired plant for Sargent.

In 1911, Sargent urged Palmer again to collect professionally and for a more extended period than the snatched weekends and his annual two week vacation, which had been the only available time previously. The letters speak for themselves:

> You have a salary, I understand, of $50 a month in your present position and I understood from you that you were rather anxious to get a couple of months next summer to look after some changes and improvements in your house. It has occurred to me that possibly you might be willing to give up your present position for six months, beginning March 1st, and devote March, April, May, June, September, and October to collecting for the Arboretum, taking July and August for your own work. We could offer you the same salary that you have now and of course pay all your traveling expenses.
>
> If you can see your way to accepting such an offer, I should want you to go to Texas to look after some *Crataegi* there in March and then gradually work northward. There are indications in southern Missouri of a large number of still undescribed species of *Crataegus* of which we have incomplete material. I should be very glad to get these doubtful species cleared up and generally to get as much work done in southern Missouri, Arkansas, and eastern Texas as time will permit. I am very anxious to get this work done and I don't know any one so well fitted to do it as yourself, so I hope that I shall get a favorable answer to this letter. (December 20, 1911)

ARNOLD ARBORETUM ARCHIVES

A sketch by E. J. Palmer of hawthorn (*Crataegus*) leaves and fruit.

And, only a few weeks later:

> … My idea is that the proposed field work would take practically all the time from March 1st to December and January unless you wanted, as I had supposed, a couple of months at home in the summer for your work.
>
> I hope this arrangement can be made for I feel very strongly the importance of it and that you are the best man for the work. If the proposition I made you does not appear satisfactory, let me know just what you want. I think if possible we ought to decide pretty soon because my idea would be for you to go to Texas early in March and it will take some time to properly lay out the campaign, etc. In any case do not let this thing fall through if there is any possible way of preventing it. (January 11, 1912)

Another negative answer from Palmer prompted this reply by Sargent:

> I am very much disappointed at your inability to devote the summer to botany and I am still in hopes that some arrangement may be made. The situation is this. We have indications of a large number of new species of trees and shrubs in southern Missouri, Arkansas, and eastern Texas. To collect these intelligently it is necessary that the collector should be in a position to visit the localities in the spring and autumn. Bush cannot be depended on for this as he is often tied up by his business. The result of this in the past has been that we have hundreds of incomplete specimens. I do not see why, if you want to take up botany, you cannot have summer employment for three or four years at least, and possibly make as much or more than you do now with the possibility that this work might lead to something better in the future. Of course if you collected for the Arboretum you could at the same time do what Bush

A New Genus

In 1913 Palmer collected an unknown plant in Jasper County, of which Bush wrote, "Do not send out any of No. 3921, and if you have any more of it, please send me all of it until I can get it described … This is a new genus to be known as *Geolobium minimum* … I have found many new species, but never a new genus, and a genus so peculiarly situated, with no known relative, no known family to receive it." The name *Geolobium* was dropped in favor of *Geocarpon* and the plant was described by Kenneth Kent Mackenzie (to whom Bush apparently sent it for identification) in 1914. Mackenzie placed it in Aizoaceae, the fig-marigold or ice plant family, but it was changed much later to Caryophyllaceae, the pink family.

Incidentally, it appeared that at least some of Palmer's botanical employers were annoyed that the description of the plant had fallen to Mackenzie, who was a lawyer and amateur botanist allied with the New York Botanical Garden. His connection with Palmer was an indirect one through Bush. While the United States had been a gold mine of new genera for a few hundred years, by 1913 a new genus was fairly uncommon (among phanerogams, certainly) and to have one get away to another institution hurt more than a little.

BRENT BAKER, ARKANSAS NATURAL HERITAGE COMMISSION

Geocarpon minimum is a tiny (less than 2 inches [5 centimeters] tall), fleshy plant that grows natively in a limited number of sites in Missouri, Arkansas, Louisiana, and Texas.

Hendrix College Herbarium
Flora of Arkansas
SAXIFRAGACEAE
Saxifraga palmeri Bush

Arkansas; Faulkner Co.; 35.28862° N. -92.48418° W; Cove Creek Preserve, 2 yds. before creek bridge on left fork of trail loop; Elevation 279 ft.

Densely growing trailside in rich, clay soil about 6 yds. from creek; in bright or mottled morning sun; with mosses, next to tree trunks and rocks; also abundant deeper into oak forest.

J. del Sol # 12 14 March 2013

HENDRIX COLLEGE HERBARIUM

Palmer's saxifrage (*Saxifraga palmeri*, syn. *Micranthes palmeri*) is one of several plants named in honor of E. J. Palmer, this species by his colleague Benjamin Franklin Bush. This small herbaceous plant grows on rocky sites in open woodlands in Arkansas and Oklahoma.

> did, make sets for yourself and sell them with the understanding that they were not to be distributed until the plants had been named. I wish you would give this matter serious consideration for I think it is of the utmost importance to American botany that these collections should be made and I feel sure that the chances for you in advancements in the next few years would be better than what they would seem to me to be if you remain as a clerk in Webb City. Perhaps you can at least tell me what sort of a proposition you might want if you are not satisfied with the one I have made. (February 1, 1912)

Bush wrote Palmer in April 1912, after a visit, that he wanted to show Palmer over the collecting ground because it was likely that he would succeed Bush in the field. Bush also wrote, "You know more about them [*Crataegus*] than I do or anyone else does for that matter." However, Palmer did not yet accept an offer from Sargent and in May Sargent wrote, "I am still most anxious that you should be connected with the Arboretum as a collector and I shall never lose an opportunity of suggesting to you the desirability of your accepting my propositions."

Again, early in 1913, Sargent wrote:

> I am in a position now to arrange permanent botanical employment for you for a period of at least three years at a salary which will be in advance of what you are now getting. I think this is a proposition which you ought not to hesitate to accept even if you are tied up in mining ventures, which you can certainly turn over to some one else. Before deciding either to accept or refuse this offer I want to talk it over fully with you and I suggest that you come to Boston at once, at my expense, and remain here for a few days at the Arboretum.... The sooner you come the better, for the offer, if you accept it, means the beginning of work in the early spring ..." (January 20, 1913)

Palmer's quick negative reply elicited this response from Sargent:

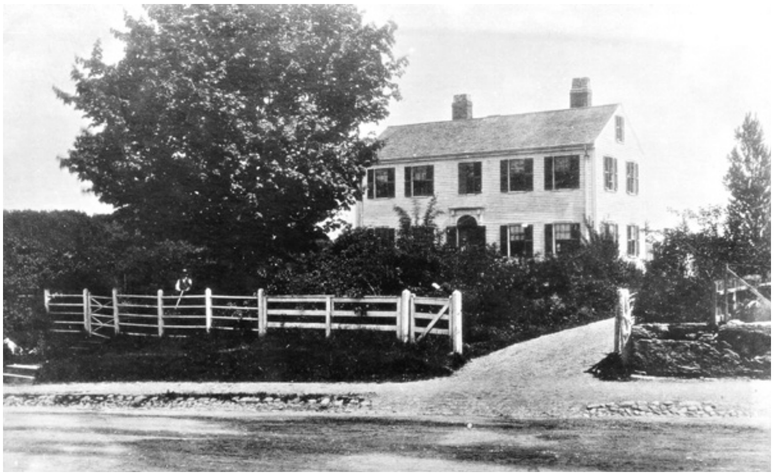
> I regret extremely that you do not see your way to taking up botany as a profession. I wanted to open a way for you to have a really distinguished career and one that

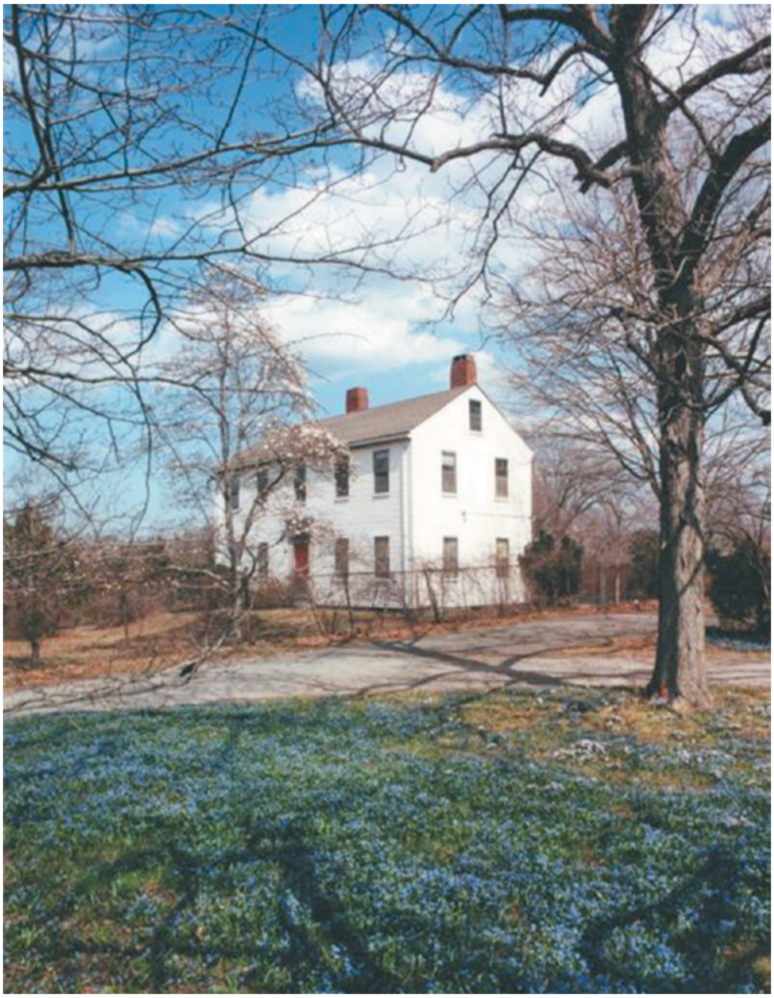
> would have paid you better than your present occupation. Mining properties are terribly uncertain and in nine cases out of ten, I am afraid, they lead to loss and disappointment.
>
> I had supposed that if you saw your way to accepting my proposition you would make your headquarters in St. Louis, and that your mother and sister would move there where I believe they would find life as comfortable and pleasant as in Webb City. I cannot tell you how disappointed I am at your decision. (January 28, 1913)

In a letter from Palmer to Sargent on March 31, 1913, Palmer again declined Sargent's request, though this time he left open the possibility of future work, writing:

> I am situated just as I was when I wrote you a few weeks ago, and I do not see how it would be possible for me to get away from here at present. I could not leave or dispose of my mining interests at this time without sacrificing all that I have put into them. However, I expect to know within a few months whether I shall realize anything on my investment or not, and it has been chiefly on this account that I have delayed making any change in my plans for the past year. As I am situated in Webb City, with my mother and sister here and some property to look after, I can scarcely see how I could manage to be away altogether. However, I expect to make a change of some sort shortly, but not likely before fall. If there is still an opening in the line you suggest at that time I might be in a position to take advantage of it, but could not possibly do so just now.

ARNOLD ARBORETUM ARCHIVES





The farm house at 1090 Centre Street is seen in a black-and-white photograph from the early 1900s and a contemporary view, photographed around 2000 by the author's childhood friend, Henry Alfred Anderson.

His resistance was fading, however, and he wrote to Sargent on June 20, 1913, "While it would be more advantageous to me in my present financial circumstances to retain my present position until spring I scarcely feel that I should put you off any longer if you feel that the work to be done this year is urgent, and I am to undertake it." He finally began working as a collector for the Arnold Arboretum and Missouri Botanical Garden later that year. The death of his father on September 17, 1911, after a long illness, probably made this easier.

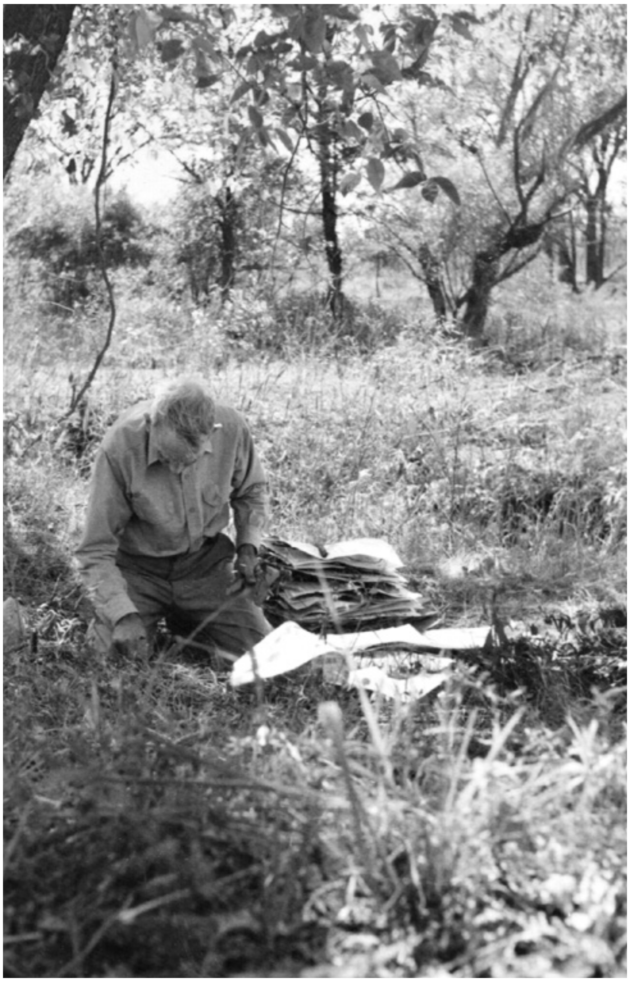
Moving to Boston

It was not until after his mother, Anna Windle Palmer (born 1841) died on April 30, 1920, that Palmer felt free to move to Boston. Finally at 11:00 p.m., April 4, 1921, a cold and rainy night, at age 45, Palmer arrived in Boston. He had never visited an eastern city before and knew only Sargent in the whole of Boston.

The next day, Palmer called on Sargent before noon. (That evening he wrote his sister that the $1.50 he paid for a simple breakfast put him "on the road to bankruptcy.") The small Arboretum staff (all paid quite modestly) had been looking for an apartment for Palmer when he arrived. The best that they had found was a two-room suite upstairs in the house of the superintendent of the grounds, Christian Van der Voet, some distance from a place to eat.

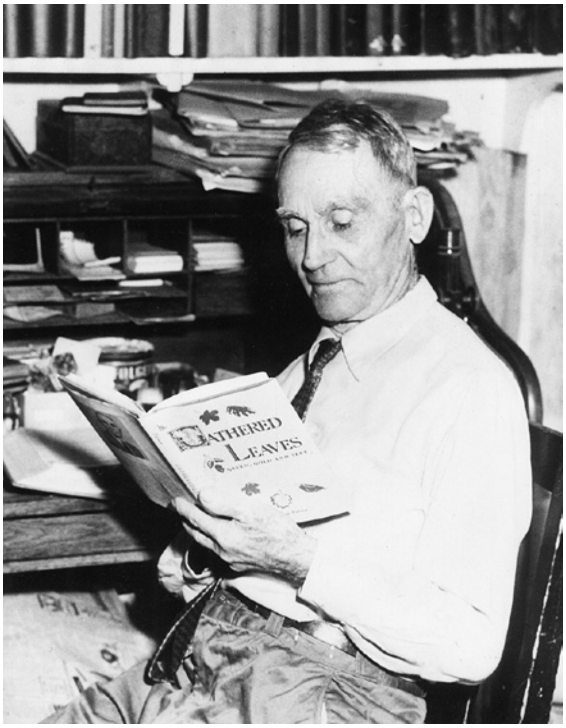
At the Arboretum, Palmer worked six and a half days a week. That half day, Sunday morning, was the most important time since Sargent arrived usually before 8 a.m. (and therefore so did Palmer). They enjoyed working together for a relatively uninterrupted few hours. Generally no one else was there on Sunday to consult the great professor. Every day Palmer rose in the morning about 5:30 a.m., spending about an hour before going out for breakfast. Then he worked until 12:30 or 1:00 p.m. when he had a small lunch at a food stand near the Arboretum. After dinner at a restaurant, he took an evening's walk, bought the newspaper, and went home to read. When the weather permitted, on his afternoon off, Palmer explored Boston on foot. (Besides relishing the exercise, Palmer deplored the high price of a trolley ride: ten cents.) Through the years Palmer continued to go on plant collecting expeditions as well as working in the Arboretum's collections and herbarium, and writing extensively on plants and other natural history topics, including the Native American artifacts he collected on the grounds.

Sargent's death in March 1927 was very distressing for Palmer. He had lost a friend and mentor and then, as of April 30 that year, Ernest Henry Wilson terminated Palmer's job, purportedly as a cost cutting measure (by Wilson's estimation the Arboretum was $120,000—nearly 1.7 million in today's dollars—in debt at the time of Sargent's death). Harvard botanist Oakes Ames (1874–1950) was appointed Supervisor of the Arboretum in June 1927, and



COURTESY OF THE AUTHOR

E. J. Palmer, at age 78, putting plants in a herbarium press while out botanizing, which he did regularly long after retirement.



ARNOLD ARBORETUM ARCHIVES

E. J. Palmer reading his poetry book, *Gathered Leaves, Green, Gold and Sere,* at home in Missouri.

Wilson was appointed Keeper at about the same time. Ames and Palmer had already established a good relationship and with Ames now as Supervisor, Palmer was rehired by 1928.

In 1930, at age 55, Palmer married Elizabeth McDougal, a bacteriologist at the Massachusetts State Laboratory, which is located to the east of the Arboretum. They had three children—my brother, sister, and me. Ames arranged for the family to live in the house at 1090 Centre Street, owned by Harvard University but adjacent to and controlled by the Arboretum.

My father's stories when I was a young child left no doubt that he and Sargent had greatly enjoyed each other's company. Throughout his career Sargent managed to enlist a number of people down on their luck in a variety of ways to become part of his "band of brothers" and sisters. During Palmer's collecting years, Sargent repeatedly made arrangements to spend a few days with him in the field. Wealthy men like Sargent who enjoy the luxury of many servants often also enjoy proving that they can get along well on their own in primitive situations.

Palmer officially retired from the Arboretum around midsummer in 1947, but returned to work in the herbarium from September of that year until early summer 1948. Palmer and his family then moved back to the family home in Webb City, Missouri. He continued to work on botany and other natural history interests seven days a week, despite declining eyesight. On his death bed, he dictated the last few words of a botanical article about his beloved Ozark forest to his wife, Elizabeth. He died hours later, on February 25, 1962. Palmer published more than 100 botanical papers in his career. Academic writing was not his only forte, though—in 1958, Elizabeth gathered seventy-six of her husband's poems, the result of his lifelong love of poetry, and published them in a volume titled *Gathered Leaves, Green, Gold and Sere.*

Acknowledgements

My wife, Laramie Palmer, began writing a Master's thesis on my father for the University of Kansas in 1970. I have freely used her extensive but unfinished manuscript for this article and in a biography I hope to publish commercially in which she is acknowledged as co-author. She should be recognized as co-author here, but I wanted to be able to say "my father."

The many letters between Sargent and Palmer are in the Arnold Arboretum Archives. Palmer kept copies also and my family donated them to the State Historical Society of Missouri. I have received permission from both institutions to quote from the letters.

Bibliography

Bush, B. F. 1895. A list of the trees, shrubs, and vines of Missouri. *Missouri Horticultural Society Report,* pp. 353–393.

Kobuski, C. E. Ernest Jesse Palmer, 1875–1962. *Journal of the Arnold Arboretum* 43: 351–358.

Palmer, E. J. 1937. Benjamin Franklin Bush. *American Midland Naturalist* 18(3): 1–6.

Sargent, C. S. 1905. *Trees and Shrubs: Illustrations of new and little known ligneous plants.* Boston and New York: Houghton Mifflin Company.

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From Fungi to Forests: The Tale of Tropical Tree Diversity

Meghna Krishnadas

Think biodiversity and a tropical rainforest might come to mind. Wet tropical forests, the most species-rich ecosystems on earth, are estimated to support nearly half of all known terrestrial species. Trees are a particularly diverse group of organisms in wet tropical forests and some regions like the Amazon can host over 1,000 different tree species in a single hectare of forest. Ecologists have long pondered the mechanisms underlying such astounding variety (Wright 2002). How do so many organisms of such similar, albeit simple, requirements coexist in such diversity in close proximity? It appears that the answer might partly lie in plant pathogens (Muller-Landau 2014).

How pathogens regulate the diversity of trees is a remarkable ecological tale. But, to better understand this story, we need to make a short trip down a path of scientific hypotheses. Many ideas have been posited to explain the conundrum of how multiple species coexist at relatively small spatial scales to generate diversity. Broadly, diversity can stem from mechanisms classified as stochastic or deterministic. Simply put, stochastic mechanisms are happenstance.

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Forest fragmentation creates edges, and edge effects occur when differences in habitat conditions in relation to distance from edge also change ecological communities.

Germinating seed of *Drypetes oblongifolia,* an evergreen tree native to the Western Ghats in southern India.

Seeds being matched to seedlings in the greenhouse.

Would a seed arrive at a spot? Would a seedling be accidentally killed by a falling branch or underfoot a roving deer? In contrast, deterministic mechanisms, as the term suggests, are processes that govern species' survival in predictable ways, such as availability of necessary resources or susceptibility to pests, pathogens, and predators (Freckleton and Lewis 2006).

The interaction between plants and their consumers and plants and pathogens has been suggested previously as an important driver of plant diversity. Only recently, however, have the links between pathogens and plant diversity been demonstrated through empirical experiments.

The Natural History of Natural Enemies

Predators and pathogens regulating population numbers of their prey or host is a well-known concept in a variety of ecosystems. In rivers, lakes, seas, or forests, predators keep consumer numbers in check. As with larger animals, predators of seeds and seedlings also exert a top-down effect on plant populations, and wet tropical forests are home to a variety of insects and fungi that kill seeds and seedlings. The forest understory provides especially conducive settings for fungi. Thriving in the wet, dark forest floor, soil fungi infect seeds and seedlings, thus regulating their numbers. In a surprising twist, however, by keeping down the numbers of their hosts, plant predators allow other species to persist, thus promoting diversity of plant communities.

Pathogens act in a manner termed "negatively density dependent." Negative density dependence just means that an individual plant is more likely to be infected by its pathogen when in the vicinity of its own kind, i.e., other individuals of the same or closely related plant species (Freckleton and Lewis 2006). Just as human diseases spread more when humans crowd together, increasing individuals of a single plant species cultivates the soil for the very pathogens that kill the plant's seeds and seedlings. So, when a species becomes numerous, its individuals are more likely to die, allowing less competitive species to persist, leading to a more diverse community.

Back in 1971, negative density dependence as a mechanism for diversity in multispecies communities was proposed independently by Janzen and Connell, for tropical rainforests and coral reefs, respectively (Janzen 1971). The Janzen-Connell (J-C) hypothesis states that diversity of a community is maintained in part by the parasites and predators that cull young

Roads and other linear clearings fragment forests and the resulting edge effects alter the recruitment dynamics of plant communities.

A hard edge where forest abruptly transitions to a field; habitat conditions are very different for seedling establishment here.

progeny, especially where host numbers are high. Specifically, mortality of seeds and seedlings of a species will be higher with increasing numbers of that species in a neighborhood (such as close to seed-producing adult trees), opening up these spaces for other species to occupy, thus promoting diversity.

A recent meta-analysis—an analysis of the net outcome from multiple studies conducted in different ecosystems—found that overall empirical evidence supported the J-C hypothesis (Comita et al. 2014). However, the J-C hypothesis was largely tested in the context of insects and mammalian seed predators, although evidence was mounting that fungal pathogens were also crucial agents of negative density dependence. Notably, no study had explicitly tested whether density-dependent culling by seed and seedling predators actually increased diversity of the plant community.

Then in 2014, in a seasonally wet forest in Belize, researchers demonstrated how the plant community changed if the action of insects and fungi was experimentally inhibited using insecticide and fungicide (Bagchi et al. 2014). Without insects, the community of recruiting seedlings was markedly different from the naturally regenerating community. Without fungi, the diversity of seedlings dropped sharply in relation to natural regeneration.

Clearly, pathogens drove diversity of the tree community in this neotropical forest. But would insects and fungi play the same role in other closed-canopy forests? Moreover, insect and fungal communities vary with factors like light and moisture—factors that also affect plants directly. How would pathogen impacts on plant diversity and composition change with different habitat conditions brought about from different light and moisture levels? Importantly, with environmental conditions changing rapidly because of human actions, how would maintenance of plant diversity via pathogens change in human-altered forests (Swinfield et al. 2012)?

What Happens When Humans Alter Forests?

We live today in a human-dominated planet. For food, fuel, and other natural resources, humans have deforested much of the earth, breaking once-large and contiguous forest into smaller parcels, a process known as forest fragmentation. One of the greatest threats to biodiversity, forest fragmentation sets in motion a range of ecological processes that alter the dynamics of species' survival in the remnant forests.

Long-term research in experimentally and naturally fragmented forests have found that fragments often lose species in predictable ways (Laurence et al. 2011). Edge effects, or altered habitat conditions at forest edges, are strongly associated with changes in fragmented tree communities. At edges and in smaller fragments, slow-growing, dense-wooded, shade-tolerant tree species are lost over time, being replaced by fast-growing, light-loving species. However, while patterns of species' losses are clear, the underlying mechanisms are less well understood (Didham et al. 2012).

Human activities like agriculture are another major cause of forest fragmentation and change in ecological communities

A typical human-dominated tropical landscape where forests exist in a matrix of farms, roads, and human habitations

Hitherto, edge effects have been primarily examined as changes to abiotic conditions—alteration in light, moisture, wind speed, etc., as we move from the forest edge to interior. Because species differ in their ability to survive in different levels of these resources, changes to light or moisture are assumed to alter species survival at different distances from edges. As a consequence, the plant community changes at edges compared to interior forest. Such changes in the tree community have important consequences for ecosystem functions such as carbon storage or nutrient cycling (Chapin et al. 2000). Hence, grasping the mechanisms driving community-wide changes to trees could improve management and inform restoration of fragmented forests for tree diversity and ecosystem function.

So why are edges dominated by light-wooded, early successional tree species? Let us suppose that edges behave like giant forest gaps. Light-loving, fast-growing species often colonize and dominate gaps by exploiting the high resource conditions. But, once the canopy is established in a gap, light availability reduces and more shade-tolerant species are able to come in. Without abundant light, the light-loving species do not have the resources to grow fast and are outcompeted by slower-growing species.

Events unfold differently in forest edges. Even after the canopy forms, shade-tolerant species seem unable to establish at edges. It is argued that high light at edges disadvantages slow-growing, shade-tolerant species, and fast-growing species outcompete them. As a consequence, edges and small fragments, which are subject to edge effects, remain dominated by light-loving species while shade-tolerant species are unable to regain a foothold. However, it is also possible that this "arrested succession" is happening because of changes to pathogen activity.

Light-loving species tend to be more susceptible to pathogens than shade-tolerant species, although there are exceptions. While light-loving species might initially increase in areas of high light, their numbers should start coming down when pathogens build up around them over time. Thus, in edges of older fragments, the seedlings of abundant light-loving species should suffer higher mortality from pathogens, opening up that space for shade-tolerant species. However, warmer, drier conditions at edges might reduce pathogen activity, thus diluting the mechanism that prevents one of few species from becoming super abundant. Alternatively, the benefits of high light per se help overcome losses to pathogens for all species. In this case, no species will be much affected by pathogens at edges and controlling pathogen activity would not improve survival of shade-tolerant versus shade-intolerant species.

Plant–Pathogen Interactions in Fragmented Forest

In a fragmented, human-altered forest, I examined whether and how the influence of pathogens during seedling recruitment (establishment and survival of seedlings) varied with distance to edges. The research site was within the Western Ghats Biodiversity Hotspot in Karnataka state, India. To test whether light alone or a combination of light and pathogens regulated seedling recruitment, I set up groups of seedling plots at increasing distances from the forest edge. Each group consisted of two seed traps and five seedling plots. In each

A one-by-one-meter plot where seedlings have been tagged and identified.

Plots were demarcated and labeled at their diagonal ends using PVC pipes, colored ribbons, and a location code.

A tagged seedling of *Litsea floribunda* infected by leaf fungi, resulting in a nectrotic spot.

New recruits (seedlings) were censused and tagged twice during the experiments.

group, one plot each was sprayed with fungicide, insecticide, fungicide plus insecticide, and water, and one plot was retained as control without any spraying. I set up 145 such groups at 15 locations, three groups each at distances of 0, 25, 50, and 100 meters (0, 82, 164, and 328 feet) from the edge, totaling 730 seedling plots. I applied pesticide treatments from November 2015 through November 2016. During this time, seeds falling into the seed traps were recorded twice a month. I conducted censuses for new recruits twice during the year: once at the end of the dry season and then at the end of the wet season after peak recruitment occurred.

Preliminary results indicate that seedling diversity reduces when plots are sprayed with fungicide, but only as we move into interior forest. Similarly, turnover of species between seeds that arrive at a spot and seedlings that establish is lowered with fungicides, but only in interior forest. Importantly, the density-dependent effect of fungi and insects appears to be at play only in interior forest. Hence, it appears that the lower diversity of seedlings in plots with pesticides are likely due to a loss of pathogen-mediated mortality of seeds and young seedlings as we move towards the forest edge. Clearly, edge effects are changing some interactions between plants and their pathogens, which in turn appears to be affecting the diversity of the plant community.

The Future of Diversity

Uncovering the mechanisms driving diversity remains a fascinating quest. You know you have stumbled upon a rich question when every answer opens up more questions. But, as we slowly piece together bits of the diversity puzzle, we are also changing natural systems at an unprecedented scale. Labeling the "Anthropocene" as a valid geological epoch awaits scientific consensus, but few can miss the ubiquitous influence of humans on Earth (Corlett 2015). Human actions have wiped out entire species, introduced new plants and animals to places where they were unlikely to reach, changed species' numbers in relation to one another, and altered biological communities in a blink of evolutionary time. Unless we apply some serious course correction, today's biodiversity might stand a bleak chance for tomorrow. Even if we set aside areas of land and water for other species, much of Earth will likely continue to be occupied by *Homo sapiens* in the near future. One hopes that by understanding the subtle processes that generate diversity, we can better manage the spaces that we share with other species, both for biodiversity and its contribution to human needs.

Bibliography

Bagchi, R. et al. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506: 85–88.

Chapin, F. S. et al. 2000. Consequences of changing biodiversity. *Nature* 405: 234–242.

Comita, L. S. et al. 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology* 102: 845–856.

Corlett, R. T. 2015. The Anthropocene concept in ecology and conservation. *Trends in Ecology and Evolution* 1–6. doi:10.1016/j.tree.2014.10.007

Didham, R. K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121: 161–170.

Freckleton, R. P. and O. T. Lewis. 2006. Pathogens, density dependence and the coexistence of tropical trees. *Proceedings of the Royal Society, Biological Sciences* 273: 2909–2916.

Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2: 465–492.

Laurance, W. F. et al. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144: 56–67.

Muller-Landau, H. C. 2014. Ecology: plant diversity rooted in pathogens. *Nature* 506: 44–45.

Swinfield, T., O. T. Lewis, R. Bagchi, and R. P. Freckleton. 2012. Consequences of changing rainfall for fungal pathogen-induced mortality in tropical tree seedlings. *Ecology and Evolution* 2: 1408–1413.

Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.

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Fraxinus bungeana: An Ash of a Different Color

Anthony S. Aiello

Fraxinus bungeana, Bunge ash, is a plant that challenges one's preconception of a genus because, unlike other ashes, this Chinese native is a shrub with showy flowers instead of a tree with inconspicuous flowers. It belongs to a group known as the flowering ashes, which includes the better-known *F. ornus* along with the Asian *F. sieboldii* and *F. chinensis.* Its flowers and form are more reminiscent of its oleaceous cousins, *Syringa* (lilac) and *Chionanthus* (fringetree), than they are of familiar members of its own genus. This species has been cultivated in botanic gardens since the late 1800s, but has never significantly jumped the fence into general horticulture.

Fraxinus bungeana is native to north-central China, where it grows in dry sandy soils and rock crevices. It was first collected by intrepid Russian plant collector Alexander von Bunge in 1831 on one of his explorations of Siberia, Mongolia, and Beijing. It was subsequently given its species name by botanist Alphonse de Candolle in 1844. Additional herbarium records appear throughout the latter half of the eighteenth century, but the first known seed introduction into North America was to the Arnold Arboretum in April 1880 from the Muséum National d'Histoire Naturelle, in Paris. A second collection was received by the Arboretum in January 1882, from Emil Bretschneider, a physician and botanist who explored the plains and mountains surrounding Beijing. Remarkably, one plant (accession 14625*A) from this collection is still alive, located in the ash collection on the east side of Bussey Hill. As of July 2017, this tree had a height of 12 feet (3.7 meters) and spread of 16 feet (4.9 meters).

The next wild collections after Bretschneider's were those of the USDA's explorer, Frank Meyer, who collected seeds in late 1907, again in and around Beijing. As far as can be determined, none of Meyer's plants remain alive. Meyer aptly described it as, "an ash growing in rocky situations and on steep mountain sides. Attains, apparently, no great size. May be of use as a foresting plant in semiarid regions." In light of the spread of emerald ash borer, and as part of recent efforts to increase the diversity of ashes in the United States, collections of *F. bungeana* seeds were made in 2009 by Kang Wang, Beijing Botanical Garden, in Liaoning, Hebei, and rural Beijing municipality, and the following year by Kang Wang, Michael Dosmann (Arnold Arboretum), and I, near Beijing, as part of the 2010 North America-China Plant Exploration Consortium expedition (collections NACPEC10-039 and NACPEC10-042).

Bunge's ash is a large shrub, growing 6 to 15 feet (1.8 to 4.6 meters) tall. The plants from which we collected in China in 2010 were 3 to 6 feet (0.9 to 1.8 meters) tall. As mentioned above, it has small, terminal flower panicles with small white fine-petaled corollas that resemble those of fringetree. Alfred Rehder, in his *Manual of Cultivated Trees and Shrubs,* described it as a "distinct species, handsome in bloom." This year I noticed seed production for the first time on one plant at the Morris Arboretum. Fall foliage color is at best similar to forsythia, with purple overtones fading to yellow. As with other ashes, Bunge ash prefers full sun, and seems adaptable to a range of soil pH. It clearly can tolerate dry conditions but also thrives in rich soils. It is likely cold hardy through USDA Zone 5 (average annual minimum temperature -10 to -20°F [-23.3 to -28.9°C]).

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Cultivar description: *Fraxinus bungeana* 'Sunflash'

Growing plants from seed can result in a great amount of variation, providing the opportunity to select for vigor and health and, occasionally, to find novel plants. This was the case in September 2014 when I first noticed a variegated plant among a group of seedlings from the NACPEC10-042 *Fraxinus bungeana* collection (Morris Arboretum accession number 2010-213*A). This plant, which has not flowered yet, has a growth rate and habit similar to others collected in 2010, but differs in having leaves that are patterned with a mixture of green, yellow, and cream. This variegation has been consistent since it was first observed and persists throughout the season. We are currently working on propagating this individual for further distribution.

***Fraxinus bungeana* 'Sunflash'**

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