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# Analysis of Switchgrass Reveals the Hitherto Secret Existence of a Unique, Local Genetic Line

**BY CAROL AUER**

Switchgrass growing in a roadside and in the coastal zone in Connecticut. Photo Credits: Geoffrey Ecker and Patrick Lienin.

**SWITCHGRASS** (*Panicum virgatum* L.) can be found in Connecticut's coastal habitats as well as along many highways. It's a native grass that humans have transformed into a cultivated plant for erosion control, gardens, and biofuels production. But why is this coastal grass abundant in roadsides and disturbed sites? What can switchgrass DNA tell us about these populations in today's human-dominated landscapes? Our research hypothesis was that seed dispersal from plants in the coastal zone had created persistent switchgrass populations throughout the state. The results provided two unexpected conclusions: our region contains a coastal switchgrass population that is genetically unique, and many roadside plants are more closely related to prairie populations than coastal populations. Most importantly, this project emphasizes the importance of remnant coastal plant communities because they can contain secret pockets of genetic biodiversity.

Switchgrass has a huge distribution range that extends southward from Canada through the eastern and central U.S. to Mexico, Cuba, Bermuda and Costa Rica. It is a perennial, warm-season ($C_4$) bunchgrass about 0.5-3 m tall. Its widespread distribution speaks to its adaptations to drought, salt, cold, and other harsh conditions. In Connecticut, studies by Niering, Warren, and others showed that switchgrass is native to a narrow, upland zone along coastal salt marshes.[1] However, our first botanical survey showed that switchgrass now occurs in roadsides and disturbed areas throughout Connecticut.[2] Our second survey across New England confirmed that populations grow inland as much as 188 km from the coast.[3] Through statistical analysis of collected specimens, we showed that roadside switchgrass plants were positively correlated with warmer temperatures, lower elevations, urban areas, sandy soils, and acid soils (lower soil pH). In general, switchgrass plants were more frequently observed closer to the coast. These botanical surveys raised many questions about switchgrass genetics, adaptations, ancestry, and dispersal mechanisms.

A history of wild switchgrass collection, breeding, and genetic engineering has resulted in the development of many genetic lines (cultivars) that grow vigorously under different environmental conditions (Table 1). These switchgrass cultivars have been used for coastal restoration, wildlife habitat, ornamental gardens, wildflower meadows, roadside plantings, streamside buffers, erosion control, cattle forage, and biofuels production.

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We thank Janet Novak, Eleanor Saulys, Arieh Tal, and others for the excellent photos on the web site. CBS members are encouraged to submit web materials to: webmaster@ct-botanical-society.org.

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# Roland C. Clement 1912-2015

**BY GLENN DREYER**

**LONGTIME CBS MEMBER** Roland Clement died on March 21, 2015 at the age 102. Roland was probably best known as an ecologist with the National Audubon Society who worked his way up to being a vice president in the organization. He was with Audubon during the 1960s when Rachel Carson raised the alarm about chemicals in our environment, particularly the insecticide DDT, in her classic book *Silent Spring*. Roland became one of Carson's staunchest defenders in the face of withering attacks from the chemical corporations and their lackeys. An ornithologist and artist with a philosophical turn of mind, he held degrees in botany and geology, among others.

Roland Clement celebrating his 91st birthday at Aton Forest. Former CBS President Carol Lemmon is in the background. Photo by G. Dreyer.

Roland was always very involved in environmental organizations, committees and commissions, too numerous to mention here. I got to know him personally when we were both asked to join the board of directors of Aton Forest, Dr. Frank Egler's personal research and demonstration forest in Norfolk, Connecticut. Prof. William Niering was also on the board and we would pick up Roland and drive together to northwestern Connecticut. These were some of the most interesting conversations of my life, and I took advantage of the two hours each way to pick the brains of two of the most eminent and admirable environmentalists in country. Roland was definitely one of the best educated and most brilliant people I have ever met. Luckily he was also very friendly and had a really good sense of humor. A certifiable "bird nut" he was also an all-around naturalist and enjoyed botanizing and discussing vegetation change with people like Niering and Egler who were pretty much obsessed with the latter topic.

With CBS, Roland's main role was as an editor of our newsletter from 1999 – 2012, his 100th year! What luck for us to have someone so knowledgeable in that role. As happens with small organizations, editors are often called upon to provide content, as well as finding other authors, and luckily Roland always had something to say.

Roland was clear of mind and relatively sound of body to the end of his long life. We should all be so lucky. He will be missed by his many friends in CBS and throughout the world.

*Glenn Dreyer is CBS president.*

Left: *Anomodon attenuatus* carpets a white oak tree base to over 1 meter from the ground. Right: *Plagiomnium cuspidatum* rings a white oak tree in a dry mixed oak-huckleberry forest.

# The White Oak Effect

**BY STEVEN MESSIER**

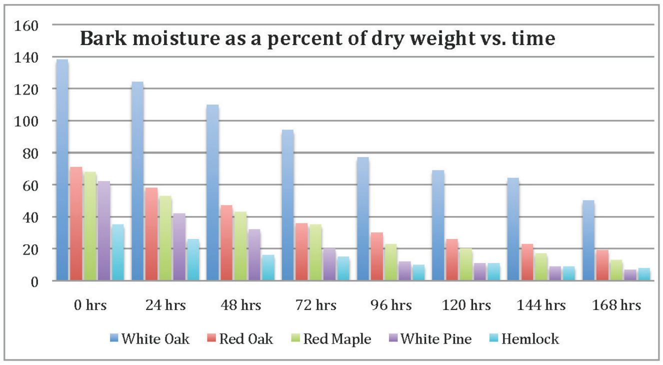
**CENTRAL CONNECTICUT'S FARMINGTON RIVER VALLEY** contains deep deposits of stratified sands and gravels. Forests of mixed oaks and pines grow on the driest sites, while moister, lower slopes have an understory of hardwoods including maples, birches, and beech.

In the moist forests of Farmington's Winding Trails Recreation Area, thick bryophyte carpets drape the bases of century-old white oak (*Quercus alba*) trees to a meter or more above the forest floor. The mosses most common to the white oaks in this community are *Anomodon attenuatus, Anomodon rostratus, Plagiomnium cuspidatum, Rhodobryum ontariense*, *Thuidium delicatulum*, *Plagiothecium laetum, Rhynchostegium serrulatum, Entodon seductrix, Brachythecium laetum, Amblystegium serpens, Callacladium haldanianum,* and the liverworts, *Cololejunea biddlecomiae* and *Frullania eboracensis*.[1, 2]

Other tree species display different communities of bryophytes. *Dicranum montanum*, *Platygerium repens*, and *Frullania eboracensis* are common to most, and about a half dozen other species occur regularly at their bases. However, unlike the impressive mats on the white oaks, these trees usually only have thin, sparse bryophyte colonies close to the ground, or hugging the cracks in the lower bark.

In the dry, mixed oak-huckleberry woodlands, *Plagiomnium cuspidatum* is only found on the soil at the bases of white oak trees. This moss usually occurs in "moist shady habitats."[3] How do white oak trees support this mesophytic moss, and such a luxuriant and diverse bryoflora compared to all the other tree species in these woods?

Phillips suggested that in dry habitats bryophytes may show host tree preference due to bark differences.[4] With this in mind, I performed an informal test to see how white oak bark differed from that of other trees. I collected bark from the bases of five species common to the Winding Trails forests, choosing large trees with a diameter at breast height (DBH) of over 60 cm. After oven drying three samples of each of their barks, I soaked them for 24 hours in a bowl of water, then let them air dry in waxed paper cups. I then weighed them daily for a week. The ability of white oak bark to retain moisture was vastly superior to that of the other tree barks tested, (see chart). After one week, white oak bark still retained 50% of its dry weight in water. Hemlock (*Tsuga canadensis*) bark had the poorest ability to retain moisture of the five trees sampled.



Moisture in five tree barks as a percentage of their dry weight, during the week following soaking. Results are averages of three samples of each type of bark from the bases of trees.

My findings parallel those of Studlar, who found that bark water-holding capacity decreased in this sequence: red oak (*Quercus rubra*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and hemlock.[5] While Studlar did not test white oak, other species I tested correlate with her data, so I assume my findings on white oak bark's water-retention capability relative to the other trees are probably valid.

Precipitation gathered by the crown of a tree that flows along the trunk to the ground is called stemflow. White oak bark is very soft and flaky compared to the other tree barks. It is also thick and corky, and tends to break free easily. These properties help it to absorb and hold stemflow for a much longer time than the hard bark of red oaks or the resinous barks of softwoods. In addition, it lacks continuous vertical channels, restricting the flow of water more than trees whose bark has furrows between plates, like white pine and red maple. Consequently, white oaks usually have small to negligible stemflow volumes.[6, 7] Trees with very smooth bark, like beech or birch, have high stemflow volumes that carry water quickly to ground where it soon drains away in sandy soils.[8] White oak bark seems to act like a reservoir providing a slow, yet prolonged release of moisture to the soil around the tree base.

White oak bark is flaky, absorbent, and lacks continuous vertical channels.

White oak and sugar maple (*Acer saccharum*) trees have more bark litter at their bases than the other deciduous forest trees.[6] This may play an important role in collecting water that does not flow directly down the trunk. Stemflow actually drips from the trunk in a diffuse pattern around rough barked trees, such that up to an additional 50% reaches the ground within a radius of 20 inches from the trunk.[9,10] Bark litter may act as an additional stemflow reservoir to augment surface soil moisture levels. Moisture retention by white oak bark may explain the presence of *Plagiomnium* in dry oak forests, as well as *Rhodobryum ontariense* and *Thuidium delicatulum*, mosses that usually prefer [even] wetter sites.

Among the bryophytes listed above for white oaks, *Anomodon attenuatus, A. rostratus, Rhodobryum ontariense*, and *Cololejunea biddlecomiae* are identified as calciphiles.[11,12,13] Why should these species grow in woods with acidic sandy soils? Carlisle et al. suggest stemflow may play a role in the growth and nutrition of bryophytes on tree stems and bases.[14]

When precipitation intercepts a tree it becomes nutritionally enriched by washing off particles deposited in the canopy and exchanging minerals from tree tissues and any associated microbiota. This latter process, called canopy exchange, varies for different ions, seasons, and tree species. Lovett and Lindberg attributed about ¾ of a 10-fold increase in the calcium concentration in the precipitation to ionic exchange within a leafy white oak canopy.[15] Most of this enriched solution drips to the ground as throughfall, but a very small percentage is diverted as stemflow. Together, they form an important pathway for nutrients to reach the forest floor.[16]

As the solution flows over twigs and branches, additional enrichment occurs from leaching of bark and microbial tissues. This effect increases with tree size due to longer travel distances down the branches and trunk.[17] White oak's very low stemflow volume increases its residence time with the surface tree organs, further extending the opportunity for ionic exchange.[18] Crozier and Boerner found calcium levels in white oak stemflow to be 64 times that of ambient rainfall. Because stemflow's volume and its chemical concentration are inversely related, beech's high volume of stemflow only showed about a 3.5-fold enrichment in calcium, while red oak and red maple increased 6- to 8-fold.[19]

On coarse-grained soils, high volumes of stemflow from smooth-barked trees like beech move rapidly through the upper soil column, carrying along with it most of the dissolved calcium. However, since stemflow is introduced to the soil very slowly from white oaks, the highly concentrated solution is exposed to the exchange complex of soil surfaces for an extended period of time, minimizing loss by leaching. This produces concentric chemical gradients around the white oak bases, similar to the "fertile island" effect found in soils at the base of some desert shrubs.[20] Crozier and Boerner found the A-horizon soil calcium concentration close to the white oak bases some 3-5 times greater than comparable measurements for the other hardwood tree species. This difference diminished to about 2:1 at 40 cm and became negligible at 70 cm from the tree bases. Soil pH followed a similar pattern, dropping from 6.8 close to the white oaks, compared to between 4 and 5.2 for the other species. The other trees showed no significant soil chemistry gradients. It is important to note that this effect of white oaks is limited to coarse-grained soils capable of high leaching rates, similar to those found at Winding Trails. Fine-grained soils negate the effect.[21]

Stemflow diminishes with the age of a tree due to changes in morphology and bark. Data for a 100-120 year-old oak stand show that less than 1% of the precipitation reaches the ground as stemflow, compared to younger oak stands at 2% to 5%.[22] Gersper and Holowaychuk could detect no stemflow for a 48 cm DBH white oak during several intense rainstorms, and radioactive tracers indicated little or no stemflow for the past 25 years.[23] Since the oldest white oaks in the Winding Trails forest exceed 100 years, with DBHs over 60 cm, it is unlikely stemflow reaches their bases. In these situations, any soil chemical gradients under rough barked trees are attributed to the presence of bark litter.[24, 25]

As the age of the forest increases, the optimal range of many bryophyte species shifts to greater heights upon the tree trunks.[26] In old-growth forests in Connecticut, Nichols found that bryophytes carpeted the bases of trees and

*Anemone americana* grows at the base of white oak with bryophyte calciphiles *Anomodon attenuatus* and *Rhodobryum ontariense*.

extended to a height of 24 meters.[27] If, as white oaks age, their bark intercepts increasing quantities of water flowing from the canopy, it may explain why mosses like *Anomodon* creep ever higher up their trunks. Over time, elevated bark concentrations of calcium and moisture levels may slowly rise up the tree trunk, providing a good habitat for moss colony growth. In addition, existing moss colonies thicken and help to conserve moisture, thus improving the humidity levels in the forest, and favoring further expansion of bryophyte growth.[28, 29]

In addition to the effects on the forest bryoflora, vascular species like wild geranium (*Geranium maculatum*) show preferential distribution around white oak trees.[30] I found *Anemone americana* plants growing in the middle of *Anomodon attenuatus* carpets at the base of two white oaks, yet nowhere else on the property. Close attention should be paid to the base of white oak trees when performing floristic surveys on coarse-grained soils.

Through a combination of very water-retentive bark, a highly reduced stemflow volume, and a large quantity of bark litter, white oaks slowly release a concentrated calcium solution to the soil at their bases. In coarse-grained soils this enhances moisture and nutrition in the upper horizons, and raises the pH close to the white oak tree base. This “white oak effect” allows mosses like the moisture-loving *Plagiomnium* to grow in Winding Trails’ dry oak-huckleberry forests, and calciphiles like *Anomodon* to produce such impressive carpets on trees in forests with acidic, low-nutrient soils.

*Steve Messier recently completed surveys of the vascular flora and bryophytes of the Winding Trails Recreation Center. Steve has led field trips for CBS since the 1980s and will offer one to Winding Trails focusing on bryophytes in October.*

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# Plants and Mycorrhizae (Part 2)
# “Cheaters” and the Myth of the Saprophytic Plant

**BY DAVID YIH**

**NEARLY ALL MEMBERS OF THE PLANT KINGDOM** associate with fungi to form symbioses called mycorrhizae. Of these plants, over 30,000 species are completely dependent upon fungi for their existence. They cannot germinate or grow into adulthood without the aid of carbohydrates supplied by fungi. Most are orchids that eventually develop green leaves. But about 500 species — including several Connecticut natives — lack chlorophyll and receive their carbohydrates exclusively from fungi for the duration of their lives. Historically, the discovery of mycorrhizae grew out of a curiosity about unusual plants like pinesap (*Hypopitys monotropa*) and certain achlorophyllous orchids, such as the bird’s-nest orchid (*Neottia nidus-avis*) of Europe. Research has confirmed that most of these plants, called mycoheterotrophs, are third-party interlopers that exploit mycorrhizal mutualisms between fungi and photosynthetic plants for their own benefit. Yet although this has been known for over half a century, many respected botanical authorities continue to perpetuate an ill-founded belief that these plants draw their nutrients directly from dead organic matter, as saprophytic fungi do.

Mycorrhizae — from Greek *mykos* (fungus) and *rhiza* (root) — are common symbioses that form between certain soil fungi and the roots of most plant species. When compatible mycorrhizal fungi and plants recognize each other and create an interface for the exchange of nutrients, they may form a variety of structures in and around the plants’ roots, depending on the species involved. Broadly speaking, there are just two main types: arbuscular mycorrhizae and ectomycorrhizae.

Pinedrops (*Pterospora andromedea*), a wide-ranging North American monotrope, photographed in Rocky Mountain National Park, Colorado. In New England, pinedrops occurs in Vermont and New Hampshire. Photo: F. Delventhal (commons.wikimedia.org)

The arbuscular mycorrhiza is the most ancient type. Its name comes from the classic shape that arbuscular mycorrhizal (AM) fungi assume inside root cells, a profusely branching form called an arbuscule. As its name suggests, an arbuscule is a miniscule tree-like shape. Under the microscope, it resembles a spreading, open-grown oak. 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. According to Smith and Read, authors of the standard text on mycorrhizae, “the earliest land plants, which had no true roots, were colonized by hyphal fungi that formed [structures] strikingly similar to modern arbuscular mycorrhizas. It is now generally accepted that the colonization of the land was achieved by such symbiotic organisms.”[1]

The creation of an arbuscular mycorrhiza begins when chemicals exuded by a plant’s roots stimulate a nearby AM 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. Inside the root, a variety of structures may develop. In 1905, the botanist Ernest-Isidore Gallaud named AM structures after plant genera he found them in. *Arum*-type mycorrhizae resemble maps of bus or subway lines: hyphae flow into the spaces between rows of cells and extend alongside them, like avenues running past city blocks, and make “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 inner plasma membrane. Instead, this membrane envelops the invading hypha and all of its branches, maximizing the area of mutual contact. It’s like pushing your fingers into an aging balloon: the rubber engulfs them, letting them into it but not through it. At this glove-like interface, plant and fungus establish a marketplace where each partner deposits its nutrients, trading them for nutrients deposited by the other.

The other main type of arbuscular mycorrhiza is the *Paris* type, which Gallaud named for a Eurasian plant genus (a relative of *Trillium*). In the *Paris* type, the fungus forms coils that look like chaotic loops of strewn intestine. An occasional small arbuscule may branch off from a coil, like a sport from a tree, but the *Paris*-type mycorrhiza has no straight “subway line” traveling along outside the cells. Instead, a coiling hypha exits one cell only to enter the adjacent one, where it forms another mass of coils before moving on again to the next cell — definitely not the express train.

Meanwhile, in the soil outside the plant root, another process begins. Energized by photosynthesized carbohydrates (photosynthate) drawn from the plant roots, the outer end of the fungus extends out into the surrounding soil.

As it extends its reach, its hyphae may branch and attenuate, forming hierarchies of larger, thick-walled hyphae and progressively finer, thin-walled hyphae. The hyphae also typically exhibit anastomosis: they repeatedly branch and fuse, forming networks — like the reticulate venation patterns in certain leaves. These networks are a highly efficient system for procuring essential plant nutrients from the soil – such as phosphorus, nitrogen, zinc, and copper — and delivering them to plant roots. The proliferating mycelium casts its net wide and often associates promiscuously with multiple plants of the same or different species, prompting scientists to write papers with playful titles like: "Changing partners in the dark," "Mycorrhizal networks: des liaisons dangereuses," and "Architecture of the wood-wide web."

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 (EM), 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. Just a look at the ABCs of genera containing at least one EM species reveals several familiar faces: *Abies, Acer, Alnus, Betula, Carpinus, Corylus.*


Pinedrops flowers at the Ortiz Mountains Educational Preserve, New Mexico. Photo: Jerry Friedman (commons.wikimedia.org)

There are several differences between arbuscular mycorrhizae and ectomycorrhizae. Unlike AM fungi, EM fungi mostly do not penetrate root cells - hence their designation as "ecto-" meaning "outer" or "external." The hallmarks of an ectomycorrhiza are a fungal sheath that densely encloses the plant's root tip, elongating as the root grows, and the "Hartig net" — a labyrinthine hyphal network that grows between the outer layers of the root's cells. Despite the vast numbers of AM 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 EM associations with only three percent of seed plants. And while all AM fungi are microscopic and subterranean, many EM fungi develop large fruiting bodies that may occur above or below ground. Those that appear above ground include many common woodland mushrooms, while the most notable of the underground-fruiting EM fungi belong to the genus *Tuber,* better known as truffles.

Is it really true that mycoheterotrophs like pinesap siphon off photosynthate from green plants via these fungal connections? During the 1950s, a pair of inventive researchers realized that they could trace the movements of plant nutrients in mycorrhizae using radioactive isotopes. E. Melin and H. Nilsson showed that soil nutrients moved through EM fungi into tree seedlings and that photosynthate moved from the trees to the fungi. Swedish investigator Erik Björkman then used this approach to see if mycoheterotrophs were piggybacking on mycorrhizae. First, he drove sheet-metal cylinders into the soil around clumps of pinesap to isolate them from any connection to nearby trees. He left other clumps as they were, to serve as control groups. Upon returning the following year, he found the control groups thriving as usual, but the isolated clumps could barely send up any flowering stalks. In a further experiment, Björkman poured glucose made from the radioactive isotope carbon-14 into the phloem of trees growing near pinesap clumps to see if carbon-14, which is rare in nature, would show up in the pinesap plants. It did. So, is pinesap a parasite of the fungus (the immediate host) or of the trees (the ultimate source) — or both? Björkman coined the term *epiparasite* to describe plants like pinesap that engage in parasitism by proxy. Others call them "cheaters," because they tap into mutualistic mycorrhizal associations without bringing anything to the table.

Approximately 500 plant species around the world are fully mycoheterotrophic. Most are epiparasites, and the majority are tropical species. According to J. R. Leake, "Orchidaceae is the largest single family of myco-heterotrophs … there are over 100 fully myco-heterotrophic species and the remaining approximately 30000 species [the green orchids] are initially myco-heterotrophic prior to developing leaves."[2] Recent experiments with dwarf rattlesnake-plantain (*Goodyera repens*) have proved that green orchids can convey carbon back to their associated fungi once they reach adulthood. Thus, they partake in mutualisms that are offset in time, like borrowers repaying a loan. But some green orchids continue drawing carbon from their mycorrhizal symbionts as adults. An example is *Epipactis helleborine,* one of two exotic orchids naturalized in Connecticut. Its symbionts are EM fungi from which it draws some portion of its carbon requirements, even as a mature plant. In fact, although normally green, it occasionally produces achlorophyllous individuals. Thus, it is difficult to generalize about orchids. They exist along a continuum that ranges from mycoheterotrophic to photosynthetic plants and includes both saprotrophic (e.g., wood-decaying) fungi and mycorrhizal fungi as symbionts.

Mycoheterotrophs tend to be forest dwellers. Scientists 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! Their flowering stalks, when they do appear above ground, have a ghastly pallor – like the emergent stalks of Indian-pipe (*Monotropa uniflora*), which W. J. Hooker once compared to white wax. Some bloom erratically, like the critically endangered European ghost orchid (*Epigonium aphyllum*), "which can disappear for up to 30 [years] between successive flowering episodes at the same site."[3]

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, they depend from the start upon mycorrhizal fungi for their survival. What dust seeds lack in size they make up for in numbers; mycoheterotrophs release vast quantities of seeds that maximize the chances that some will encounter compatible fungi. Many species grow up to be scant will-o'-the-wisps, but it would be wrong to think of all mycoheterotrophs as impoverished wraiths, barely clinging to life. Asian orchids in the genus *Galeola,* for example, "may climb to over 50 m, weigh more than 100 kg, and bear hundreds of flowers; but all their vegetative parts are yellow and nonphotosynthetic."[4]

Besides the orchids, some of the best known mycoheterotrophs are the members of Monotropoideae (the "monotropes"), a subfamily within Ericaceae to which *Hypopitys* and *Monotropa* belong. Some taxonomists also include the tribe Pyroleae among the monotropes. Western North American monotropes include the monotypic *Sarcodes sanguinea*, of which John Muir wrote, "It rises … in the pine and fir woods like a bright glowing pillar of fire."[5] Its close relative, pinedrops (*Pterospora andromedea*), has a wide range that extends to Vermont and New Hampshire, though not to Connecticut. The accompanying table summarizes the native mycoheterotrophs of Connecticut and their known symbionts.

Beyond the earthy domain of mycorrhizal research, the botanical community at large has been slow to acknowledge mycoheterotrophy. As Kerner put it in 1894, "we cannot easily familiarise ourselves with the idea of a flowering plant draining the mycelium of a fungus of nutriment."[6] Furmann and Trappe pointed out that "the widespread genera *Hypopitys* and *Monotropa* have been known to be completely mycotrophic since Kamienski's (1881, 1884) elegant papers (despite this, authors of textbooks and taxonomic treatments stubbornly persist in describing these plants as root parasites or saprophytes)."[7] J. R. Leake, originator of the term *mycoheterotroph,* called for debunking the myth of the saprophytic plant that still pervades many respected sources: "Recent botanical reference works [that] continue to refer to saprophytic plants [include] the definitive guide to the Neotropical Flora that encompasses over 30 species of these plants (Smith *et al.,* 2004) and the magnificent New Atlas of the British Flora (Preston *et al.,* 2002). The latter describes the four higher-plant species of myco-heterotrophs in the UK (*Neottia nidis-avis, Corallorhiza trifida, Epigonium aphyllum* and *Monotropa hypopitys*) as 'saprophytic perennial herbs of leaf litter'. In the latest and most comprehensive colour guide to the British and Irish flora, Blamey *et al.,* (2003) describe the same species 'as saprophytes feeding on rotting vegetation with the aid of a fungus partner'. Such explanations are entirely misleading since none of these plants derive carbon from decaying organic matter."[8] I found several more instances of the fallacy, both on the internet and among my botanical books. All are examples of a deceptively plausible idea passing, without scrutiny, from one authority to the next — more in the manner of rumor than of science. The ungreen oddity of the mycoheterotrophs seems always to have cried out for comment, but today's commentaries ought to recognize the truth of the matter at last.

Flowering stalk of the Connecticut mycoheterotrophic orchid *Corallorhiza odontorhiza*. Photo: E. Saulys.

The recently-emerged fruiting body of *Russula emetica*, an ectomycorrhizal mushroom native to Connecticut. The CT epiparasites *Monotropa uniflora* and *Corallorhiza maculata* and the green orchids *Cypripedium* associate with certain species of *Russula*. Photo: Piotr J. (commons.wikimedia.org)

Continuing research has yielded remarkable revelations about the ecological significance of mycorrhizal networks. The upcoming final installment in our series on plants and

| **Plant family** | **Fully mycoheterotrophic CT plants** | **Fungal symbionts** |
|---|---|---|
| Ericaceae | Hairy pinesap (*Hypopitys lanuginosa*) | ? |
| (subfamily Monotropoideae) | Yellow pinesap (*Hypopitys monotropa*) | *Tricholoma* >12 spp. |
| | One-flowered Indian-pipe (*Monotropa uniflora*) | Russulaceae ~2-3 spp. |
| Gentianaceae | Twining screwstem (*Bartonia paniculata*) | ? |
| | Virginia screwstem (*Bartonia viginica*) | ? |
| Orchidaceae | Spotted coral-root (*Corallorhiza maculata*) | *Russula* ~20 spp. |
| | Fall coral-root (*Corallorhiza odontorhiza*) | *Tomentella* spp. |
| | Early coral-root (*Corallorhiza trifida*) | *Tomentella* spp. |
| | | |
| | **Partially mycoheterotrophic CT plants** | |
| Ericaceae | Pipsissewa (*Chimaphila umbellata*) | ? |
| (tribe Pyroleae) | One-sided shinleaf (*Orthilia secunda*) | *Hysterangium* spp. |
| | Green-flowered shinleaf (*Pyrola chlorantha*) | ? |
| | Probably the other CT spp. of *Chimaphila* and *Pyrola.* | |
| Huperziaceae | Mountain firmoss (*Huperzia appressa*) | *Glomus* spp.? |
| | Shining firmoss (*Huperzia lucidula*) | *Glomus* spp.? |
| Lycopodiaceae | Common clubmoss (*Lycopodium clavatum*) | *Glomus* A |
| | One-cone clubmoss (*Lycopodium lagopus*) | ? |
| Ophioglossaceae | Grape ferns & moonworts (*Botrychium* - 8 or 9 spp. in CT) | *Glomus* spp. |
| | Northern adder's-tongue fern (*Ophioglossum pusillum*) | ? |
| | Southern adder's-tongue fern (*Ophioglossum vulgatum*) | Glomeromycota |
| Orchidaceae | All other CT orchids | |

**Native Connecticut mycoheterotrophs and their symbionts.**[9] Mycoheterotrophs show much more specificity in their fungal partners than other mycorrhizal plants do. The known fungal symbionts listed for the CT full mycoheterotrophs have EM connections to trees. The Glomeromycota (including *Glomus*) form AM symbioses. *Orthilia secunda* may be extirpated in Connecticut.

mycorrhizae will look at these surprising findings and examine the role of mycorrhizae in agriculture and conservation.

*David Yih is CBS vice president. He thanks Sam Saulys for information on fall coral-root.*

## Notes

1. Smith, Sally E. and David J. Read. 2008. *Mycorrhizal symbiosis,* third edition, pp. 2-3. Hyphae are the minute tube-like filaments that are the basic structure of most fungi. British authors prefer *mycorrhizas* to *mycorrhizae* as the plural form.
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8. Leake 2005:113-114 (see note 2, above).
9. Sources for the table:

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   Winther, J. L. and W. L. Friedman. 2008. Arbuscular mycorrhizal associations in Lycopodiaceae. *New Phytologist* 177(3)

## Switchgrass

*continued from page 1*

Switchgrass cultivars recommended in a Connecticut state erosion and sedimentation control manual (2002) included 'Shelter,' 'Blackwell,' and 'Cave-in-Rock'. A federal agency recommends using 'Blackwell' and 'Shelter' for our region. Thus, it is not surprising that switchgrass population genetics has become muddled across the U.S.

Switchgrass has a very high degree of genetic diversity, which is the result of polyploidy, out-crossing, and thousands of years of range expansion and diversification after the last ice age. Scientists have grouped switchgrass into two ecotypes, Lowland and Upland, with distinctive adaptations and traits. Upland plants are typically associated with dry habitats and colder northern latitudes, while Lowland plants are usually found in moist habitats in warmer southern latitudes. Lowland plants tend to be taller and coarser with a more noticeable blue-green leaf color. However, the tremendous variation between sites and individuals prevents experts from classifying plant ecotype based on appearance. Switchgrass is also a polyploidy species meaning that plants have more than two sets of chromosomes. Lowland ecotype plants are tetraploid (four sets of chromosomes), while Upland plants are usually tetraploid or octoploid (four or eight sets). As discussed below, our research has shown that local, coastal switchgrass plants are Lowland tetraploids, but many of the roadside populations have a different ancestry.

| Cultivar | Origin | Ecotype | Ploidy |
|---|---|---|---|
| Dakotah | North Dakota | Upland | 4x |
| Summer | Nebraska | Upland | 4x |
| Cave-in-rock | Illinois | Upland | 8x |
| Shawnee | Illinois | Upland | 8x |
| Shelter | West Virginia | Upland | 8x |
| Carthage | North Carolina | Upland | 8x |
| Pathfinder | Nebraska | Upland | 8x |
| Forestburg | South Dakota | Upland | 8x |
| Sunburst | South Dakota | Upland | 8x |
| Trailblazer | Nebraska | Upland | 8x |
| Blackwell | Oklahoma | Upland | 8x |
| Caddo | Oklahoma | Upland | 8x |
| High Tide | Maryland | Upland | - |
| Southlow | Michigan | Upland | - |
| Miami | Florida | Lowland | 4x |
| Wabasso | Florida | Lowland | 4x |
| Stuart | Florida | Lowland | 4x |
| Alamo | Texas | Lowland | 4x |
| Kanlow | Oklahoma | Lowland | 4x |
| SG5 | - | Lowland | 4x |
| Timber | New Jersey | Lowland | 4x |
| BoMaster | North Carolina | Lowland | 4x |
| Performer | North Carolina | Lowland | 4x |
| Southern New England Lowland Tetraploid (SNELT) | Connecticut & Rhode Island | Lowland | 4x |

Table 1. Common switchgrass cultivars, their geographic origin, ecotype, and ploidy level.

### A Study of Switchgrass Genetics in Connecticut

We analyzed switchgrass population genetics using leaf samples from 122 plants from the coastal ecoregion or inland roadsides. DNA was extracted from the leaves, and short DNA regions were amplified and sequenced. These snippets of DNA (called microsatellite markers or simple sequence repeat markers) were compared between collected individuals and a large group of reference cultivars. This provided strong evidence that many of our coastal plants (green dots in Figure 1) represented a local Lowland tetraploid genetic group. We named these local Lowland tetraploid plants 'Southern New England Lowland Tetraploid' (SNELT). In contrast, some plants (red dots in Figure 1) were Upland octoploid cultivars like 'Cave-in-Rock' and 'Shelter', cultivars developed from wild plants in Illinois and West Virginia. It is safe to assume that human activity introduced these cultivars to the landscape. The map shows an interesting north-south gradient where 67% of the inland plants were Upland octoploid and 84% of the coastal plants were Lowland tetraploid. The ancestry of 9% of the collected plants (yellow dots) could not be determined. Further details are available in our open-access publication (June, 2015) at plos.org.[4]

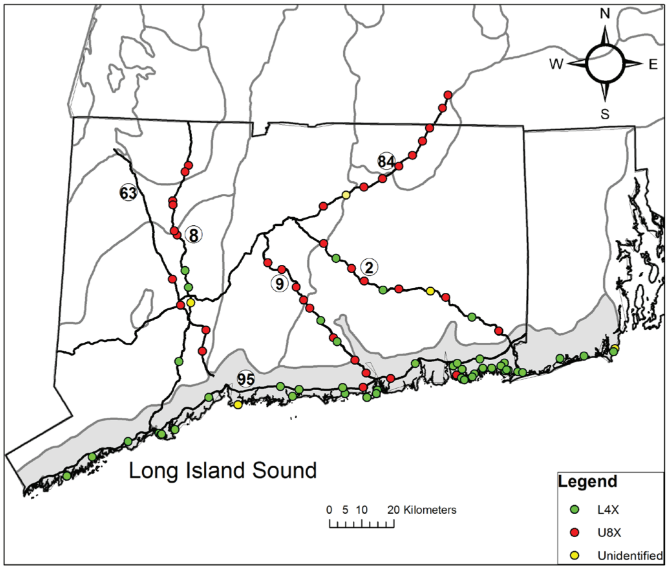

Figure 1. Map of study site and switchgrass genetic lines. Black lines represent borders of Connecticut and Rhode Island and six roads (Routes 63, 8, 9, 95, 84, and 2). Grey lines represent the borders of Level IV sub-ecoregions and the shaded area represents sub-ecoregion 59g Long Island Sound Coastal Lowland. Abbreviations: L4X, local Lowland tetraploids; U8X, non-local Upland octoploids; Unidentified, genetics not known. Reprinted with permission of the authors.

### Implications for Conservation and Biodiversity

Switchgrass has been planted in gardens, grasslands, and coastal zones without regard to its genetic heritage. Which genetic lines should be promoted in the future? Should genetic variation at the sub-species level be considered in conservation projects? Some people argue that all switchgrass plants are native and, therefore, appropriate. However, land managers have observed an aggressive tendency in some switchgrass cultivars which is probably due to their genetics. At present, science does not tell us if these non-local cultivars create significant negative effects at the community or ecosystem level. However, we have given our 'Southern New England Lowland Tetraploid' line to a local seed company for a two-year field trial. We hope that these plants will be a foundation population for a seed line for future habitat restoration projects. Our research also highlights the importance of protecting remnant, coastal plant communities because they hold unique pockets of genetic diversity of great value for future resilience.

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*Carol Auer is a professor in the University of Connecticut's Department of Plant Science and Landscape Architecture.*

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# Nickolas Nickou (1921-2015)

### BY LAUREN BROWN

**NICKOLAS NICKOU, M.D.**, a member of CBS since 1966, died on September 1, 2015. Nick, as we knew him, was a plant lover for the ages, not only knowing and enjoying the local wild flora, but also being known far and wide as a premier horticulturist. In 1960, he bought a 3-acre house lot in Branford. The property featured multiple rock outcrops, oaks that shed tough acidic leaves every fall, and plenty of bull-brier. On this unpromising site, he created and nurtured a dazzling collection of hundreds of exotic and native woody and herbaceous plants, many of which weren't "supposed" to grow in Connecticut. His specialty was "pushing the zone," coaxing one tender species after another — some only known to grow as far north as Florida — to survive and even flourish in our unpredictable and inhospitable climate. He was able to do this through an almost psychic understanding of each species' environmental needs and a Darwinist emphasis on encouraging the successful and showing no mercy for the weak. "This guy's not paying the rent," he would say of some prized but struggling exotic and out it would go.

Nick became interested in plants as a young boy, inspired by his mother's house plants and small outdoor garden. Gifted with a photographic memory, he had memorized her entire set of gardening encyclopedias by the age of 10 and would know the Latin name of any plant he later encountered whether he had seen the plant before or not. His prodigious memory amazed garden visitors, as he would rattle off the names, provenance, history, and growing requirements of one plant after another on a tour.

Rhododendrons were his special love, with over 100 species and varieties gracing the property, many of them spectacular, mature specimens. He also was interested in ferns, and experimented with breeding them. He made a cross, aptly named 'Branford Beauty,' between the Japanese painted fern (*Athyrium niponicum* var. *pictum*) and our native lady fern (*Athyrium filix-femina*), which is commercially available. All of this was accomplished on top of his working full time for over forty years as a general practitioner, in his early days making house calls, keeping office hours into the evenings, and delivering babies at night.

This short piece presents but a small view into Nick's botanical world, and others could add many more facts and stories. His horticultural accomplishments are well documented and widely acknowledged, but those who knew him will also treasure the memory of those qualities harder to describe: his deep enthusiasm, his wry sense of humor, and the mischievous twinkle in his eye.

*Lauren Brown is the author of* Grasses: An Identification Guide *and frequently leads CBS fieldtrips. She thanks Nick's friends Bruce Simonds and Fred Bland and his late-life partner Carol Hanby for assistance and material. Information has also been taken from* The Collector's Garden *by Ken Druse (Clarkson Potter, 1996). Nick's obituary may be found at* http://www.wsclancy.com/obituary/Nickolas-Nickou-MD/Branford-CT/1541549.

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All applications to become a PCV must be submitted via the online application to the Botanical Coordinator prior to training sessions. The training session for CT PCVs is March 26 9:30-4:00 at the Connecticut Forest & Park Association, 16 Meriden Rd. Rockfall, CT 06481

For more information and to apply, visit our website at **www.newenglandwild.org/volunteers/plant-conservation.html/** or contact:

Laney Widener
Botanical Coordinator
New England Wild Flower Society
508-877-7630 ext. 3204
lwidener@newenglandwild.org

## CBS Book Club

The CBS Book Club will have its first meeting during potluck lunch at the Spring Meeting. Candidates proposed for the next book to be read are:

*The Cabaret of Plants: Forty Thousand Years of Plant Life and the Human Imagination* by Richard Mabey (2016)

*Common to This Country: Botanical Discoveries of Lewis and Clark* by Susan H. Munger (2003)

*The Forest Unseen: A Year's Watch in Nature* by David Haskell (2012)

*Travels...* by William Bartram (1791)

## CBS at the International Festival of Arts and Ideas.

CBS has been invited to lead botanical walks in New Haven as part of this year's International Festival of Arts and Ideas, June 11-25. Dates and descriptions will be posted to the CBS field trip page once scheduling is confirmed.