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The Magazine of the Arnold Arboretum
VOLUME 72 • NUMBER 2

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American Chesnut.

Castanea vesca.

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Inside front cover: Illustration of American chestnut (*Castanea dentata*) from François André Michaux's *The North American Sylva,* Volume 3, published in 1819. Note that the illustration uses the old synonym *C. vesca* and an alternate spelling of the common name, "chesnut."

Inside back cover: The leaves of *Kalopanax septemlobus* accession 841-81-A, which grows near the Arboretum's Rehder Pond, developing bright greenish yellow fall color. Photo by Kyle Port.

Back cover: Fall-flowering common witch-hazel (*Hamamelis virginiana*) blooms in a Minnesota garden. Photo by Nancy Rose.

Hamamelidaceae, Part 1: Exploring the Witch-hazels of the Arnold Arboretum

Andrew Gapinski

Hamamelidaceae, the witch-hazel family, includes approximately 30 genera representing around 100 species of deciduous trees and shrubs. Members of the family are found in both temperate and tropical regions of North and Central America, Eastern Asia, Africa, the Pacific Islands, and Australia. The Arnold Arboretum has a rich history with the family, from plant exploration to the naming and introduction of its members to cultivation. The Arboretum's Hamamelidaceae collection, which currently comprises ten temperate region genera, can be found in groupings throughout the Arboretum landscape. Specific locations

KYLE PORT

Many witch-hazels display attractive fall color; seen here, *Hamamelis* × *intermedia* 'Arnold Promise' (accession 380-94-C) with red orange foliage and *Hamamelis virginiana* f. *rubescens* (accession 527-92) with yellow foliage.

All In the Family

The Arnold Arboretum currently has living specimens representing these genera within Hamamelidaceae:

Corylopsis
Fortunearia
Fothergilla
Hamamelis
Liquidambar
Loropetalum
Parrotia
Parrotiopsis
Sinowilsonia
× *Sycoparrotia*



KYLE PORT (ALL)

Chinese winter-hazel (*Corylopsis sinensis*); American sweetgum (*Liquidambar styraciflua*); Large fothergilla (*Fothergilla major*)

include the area around the Hunnewell Visitor Center, the Leventritt Shrub and Vine Garden, scattered among the trees in the North Woods, on the edges of the hickory (*Carya*) collection, near the summit of Bussey Hill, and among the jewels of the Explorers Garden.

As autumn arrives at the Arboretum, the flowering season for the witch-hazel family begins, and will carry through until spring. Starting in October, common witch-hazel (*Hamamelis virginiana*)—a New England native—begins to bloom, the straplike yellow petals of its fragrant flowers extending on warm days and curling up when temperatures drop near freezing. This show can persist into December even as the snow begins to fall. Other members of the witch-hazel genus represent the earliest of bloomers, starting in January and lasting well into March—a remarkable sight in the depths of winter.

As the ground begins to warm in April, several species of *Corylopsis*—commonly called the winter-hazels—produce many pendulous clusters of bell-shaped yellow flowers. The fothergillas (*Fothergilla*) round out the family's flowering season in the Arboretum with their bottle-brush-like white blooms in May. Beyond the showy flowering of these genera, many are also aesthetically valuable for their unique foliage, vibrant fall colors, and, in the case of *Parrotia,* attractive exfoliating bark. Given these attributes, perhaps no other plant grouping holds greater ornamental potential and yet is so underutilized in today's landscape than the witch-hazel family. This two-part article explores various historical, taxonomic, and horticultural facets of Hamamelidaceae taxa in the Arboretum's collection. We begin with *Hamamelis,* the genus for which the family is named.

Hamamelis

> Whilst winter's hand is yet heavy on the land the Witch-hazels boldly put forth their star-shaped yellow blossoms but the native *Hamamelis vernalis* is over-shadowed by its more brilliant Chinese and Japanese relatives.
>
> Ernest H. Wilson, *Plant Hunting*, 1927

Witch-hazel (*Hamamelis*) is the most well-known Hamamelidaceae genus among gardeners and includes the only native New England representative of the family—*Hamamelis virginiana,* the common witch-hazel. There are two other North American species, *H. vernalis* (vernal or Ozark witch-hazel) and *H. ovalis* (big-leaf witch-hazel), and two Asian relatives, *H. mollis* (Chinese witch-hazel) and *H. japonica* (Japanese witch-hazel). All of these

KYLE PORT

Witch-hazel flower petals can furl and unfurl depending on air temperature. Seen here are flowers of *Hamamelis mollis* 'Princeton Gold'.

ANDREW GAPINSKI

A common witch-hazel (*Hamamelis virginiana*) in fall bloom, growing in Virginia's Shenandoah National Park.


MICHAEL DOSMANN

Yellow flowers and yellow fall foliage blend on the branches of this common witch-hazel.

species are shrubs or small trees inhabiting temperate regions. They share characteristically narrow, straplike flower petals and capsulate fruit that is explosively dehiscent, capable of ejecting seeds as far as 10 meters (33 feet). Much work has been done to create hybrids (*H.* × *intermedia*) between the Chinese and Japanese species, resulting in the development of horticulturally desirable selections. Today these hybrids, as well as cultivars of *H. mollis*, are the witch-hazel family members most popular with American gardeners. Both the North American and Asian witch-hazels have a rich history, with fascinating stories of discovery and much horticultural potential.

North American Discoveries

Common witch-hazel has a wide-ranging native distribution along the east coast from Nova Scotia to Florida and west to the Mississippi River, petering out in the Ozarks. Its western limit runs from eastern Texas to Minnesota. It is commonly found in forest understories as a large multi-stemmed shrub. For non-gardeners, witch-hazel may be a familiar name not as a forest-dweller but for its use as a component in first-aid and skincare products. Native Americans used witch-hazel for its healing properties, and open-minded New Englanders soon recognized its potential. In 1866, the first commercial witch-hazel extract distillery was founded in Essex, Connecticut, by Thomas Newton Dickinson. Today, the distilling facility is located in East Hampton, Connecticut, and is the world's largest source of witch-hazel extract, still produced from witch-hazel wild-harvested from New England's woodlands.

The flowering time of common witch-hazel is definitely unique. Just as it seems that the last of the years' blooms have faded, *H. virginiana* comes into flower. Depending on the specimen in question, blooms start as early as October and can last into December. The species' fragrant flowers are composed of four yellow, straplike petals that furl and unfurl with the temperature swings of late autumn. In many cases, full bloom occurs when the plant's yellow fall foliage is still present, making it difficult to appreciate the flowers' full grandeur. This is viewed by some as an aesthetic fault of the plant, but to those who know what to look for, it is quite a remarkable display. With nothing else in bloom, the common witch-hazel has little competition for pollinators seeking a late season food source.

The Arboretum's largest concentration of *H. viriginiana* can be found in the North Woods, just past the *Aesculus* collection along Meadow Road, uphill from the short stretch of post-and-rail fence. A visit to explore this nook should be part of any autumn walk in the Arboretum. A bit farther down Meadow Road, at the northern end of Rehder Pond, is the Arboretum's oldest accession (14693-D) of common witch-hazel, wild-collected as a plant from western Massachusetts and brought back to the Arboretum in 1883 by Jackson Thornton Dawson, the Arboretum's first plant propagator.

Steps away from this specimen grows another one of the Arboretum's centenarian witch-hazels, *Hamamelis vernalis* accession 6099-D. Unlike common witch-hazel, the vernal witch-hazel, as the name suggests, flowers very early in the year (January through March). Although its geographic range overlaps with that of common witch-hazel, it only grows natively in the Ozark highlands of Missouri, Arkansas, and Oklahoma, and in small populations in Texas and Louisiana. A truly grand representation of the species, accession 6099-D was wild-collected as a seedling in Missouri and sent to the Arboretum in 1908 by Benjamin Franklin Bush under the consignment of Charles Sprague Sargent, the Arboretum's first director.

At the time of this plant's collection, *H. vernalis* had yet to be officially named and described by science, although, as herbarium records show, it was found growing in Missouri by Saint Louis botanist Dr. George Engelmann as early as 1845. Nonetheless, common witch-hazel was the only identified North American species at this point. In fact, Bush authored the 1895 publication *A list of the trees, shrubs and vines of Missouri* in which *H. virginiana* is mentioned as the sole representative of the genus. Sargent's 1890 publication *The Silva of North America, a description of the trees which grow naturally in North America exclusive of Mexico,* made the same conclusion.

The story of vernal witch-hazel's discovery begins with Sargent's and Bush's plant explorations in Missouri and Arkansas in September–October of 1907, the main goal of which was to search for new *Crataegus* (hawthorn) species. On October 8, 1907, the explorers collected a herbarium specimen in Swan, Missouri, of a *Hamamelis* in fruit, but lacking flowers; this certainly sparked their curiosity since it appeared dissimilar to the known fall-blooming species, *H. virginiana.* Returning to Boston, Sargent anxiously requested of Bush that he return to Missouri to collect seeds and flowering herbarium specimens that winter. In a letter to Bush dated January 22, 1908, Sargent wrote, "Are you doing anything about the flowers of that Southern Missouri *Hamamelis*? I am very anxious to get these this spring if possible and I am counting on you to do it, either through our friend at Swan or through your brother." Sargent received his first flowering vouchers of the suspicious witch-hazel on March 14, 1908, and wrote:

ROBERT MAYER

Flowers and old seed capsules of a 1908 accession of *Hamamelis vernalis* (6099-D) growing near Rehder Pond.

> Dear Mr. Bush:
>
> I am very much obligated for the *Hamamelis* specimens which arrived today. They were gathered a little too soon and if you had only put them in water a few days before pressing then the flowers would have fully expanded. I think there is no doubt, however, that this is an undescribed species. We want to describe and publish a figure of it in an early number of *Trees and Shrubs,* so I hope you won't "give it away" to anyone else … We must manage to get some young rooted plants of the *Hamamelis* as none of the seeds we got last autumn were good. Apparently after they were gathered they were destroyed by the weevil …
>
> Yours very truly,
>
> C. S. Sargent

Original October 8, 1907, herbarium voucher of *Hamamelis* sp. collected by B. F. Bush and C. S. Sargent in Swan, Missouri. This collection would lead to further investigation and the naming of a new North American witch-hazel species—*Hamamelis vernalis*—by Sargent in 1911. Note that the specific epithet "*vernalis*" was later added to the original description.

Vegetative specimen of *Hamamelis* from an area where *H.* X *vernalis* Sarg. and *H. virginiana* L. var. *virginiana* both occur. Positive determination uncertain, dependent upon floral structures.
Examined at Vanderbilt University in a study of variation in North American *Hamamelis* L. (Hamamelidaceae).
Gertrude E. Jenne 1965
Material from Packet
copyright reserved
Syn Type
MISSOURI.
PLANTS OF ~~INDIAN TERRITORY~~.
COLLECTED BY B. F. BUSH.
Swan, Mo.
Oct. 8, 1907.
Gravelly branches. No. 4854A.
Taney Co.
HERBARIUM OF THE ARNOLD ARBORETUM HARVARD UNIVERSITY
vernalis Sargent
Sargent, Trees & Shrubs 2:137 (1911).
det. F. G. Meyer 18 Aug. 1992
U. S. NATIONAL ARBORETUM HERBARIUM, WASHINGTON, D. C.

Hamamelis X vernalis Sarg. (pro sp.),
Trees and Shrubs 2:137. 1911.
Examined at Vanderbilt University in a study of clinal variation in North American Hamamelis L. (Hamamelidaceae).
Gertrude E. Jenne
1965
Material from Packet
Type.
PLANTS OF MISSOURI.
COLLECTED BY B. F. BUSH.
Hamamelis vernalis
Swan, Mo.
Jan. 29, 1908.
Gravelly branches.
No. 4915.
HERBARIUM
OF THE
ARNOLD ARBORETUM
HARVARD UNIVERSITY
THE HARVARD UNIVERSITY HERBARIA
00043424
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In October 1908, the Arboretum did receive and accession (6099) the rooted plants from Bush, as Sargent requested. Additional herbarium specimens of the wild plants in flower were received in February 1909 and are also held in the Harvard University Herbaria; they were undoubtedly sent to Sargent by Bush as he developed his new description of the species. In Sargent's 1911 publication, *Trees and Shrubs, Illustrations of New or Little Known Ligneous Plants,* he first described *H. vernalis* as a new species:

> The different species of *Hamamelis* offer no good morphological characters, the structure of the flowers, fruit and seeds being the same in them all. The plant, however, from southern Missouri, Arkansas and Louisiana is so distinct in its time of flowering, in the bright red color of the inner surface of the calyx-lobes, in the pale color of the under surface of the leaves, and in the amount and persistency of the pubescence on the leaves and branches that it appears desirable to distinguish it specifically from *Hamamelis virginiana.* The habit, too, of spreading by stolons into great thickets, and the fact that it grows so far as I have seen it only in the gravelly beds and margins of streams, also seem to separate it from the eastern species, which inhabits rich woodlands and upland pastures. In the color of the inner surface of the calyx-lobes and in its time of flowering *Hamamelis vernalis* resembles the Japanese species.

The individual specimen 6099-D from this original collection, which was planted and remains in its location near Rehder Pond, was first noted in bloom on January 15, 1913, by Ernest Henry Wilson, Arboretum plant explorer and "Keeper" of the Arboretum following Sargent's death in 1927. The news of the bloom was reported in the Arboretum's *Bulletin of Popular Information* that spring: "*Hamamelis vernalis* is an interesting plant with considerable decorative possibilities. It is a native of southern Missouri and, although the existence of a Witch Hazel in that part of the country has long been known, it has only recently been distinguished from the autumn flowering species of the northern states. This Missouri species flowered this winter in the Arboretum for the first time in cultivation and is still little known in gardens."

MICHAEL DOSMANN

Though not especially showy, the flowers of *H. vernalis* f. *tomentella* are notable for their fragrance.

In the 1920s, Alfred Rehder, renowned Arboretum taxonomist, described two variations (forms) of the species: *H. vernalis* f. *tomentella,* with pale, pubescent leaves, and *H. vernalis* f. *carnea,* with reddish petals. Specimens of both these forms (accessions 18885-A and 18886-A, respectively) can be found just north of the Hunnewell Visitor Center.

Astonishingly, almost one hundred years after Sargent named *H. vernalis,* a third species of North American witch-hazel was named. *Hamamelis ovalis,* known commonly as bigleaf witch-hazel, has a known range that is limited to a handful of counties in southern Mississippi and Alabama. It was discovered

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Flowering specimen of *Hamamelis vernalis* sent from B. F. Bush to C. S. Sargent, at Sargent's urgent request following their collections in Swan, Missouri, the previous autumn. The flowers are only partially opened, as Sargent pointed out to Bush in his March 14, 1908, correspondence letter.

MICHAEL DOSMANN

This specimen of big-leaf witch-hazel (*Hamamelis ovalis,* accession 114-2009-A) displays the species' distinctive red flowers.

in July 2004 during a botanical inventory of a National Guard training site in Perry County, Mississippi. Officially described in 2006, this species has several distinctive traits including varying red petal coloration, musty floral scent, relatively large pubescent leaves, and the habitat in which it is found. Although known only to the far south, it carries the hardiest aspects of its relatives, growing remarkably well here at the Arboretum. Three specimens can be found planted in the collections, including accessions 113-2009-A and 114-2009-A in the Leventritt Shrub and Vine Garden. The latter of the two in particular expresses the large leaves for which the species is commonly named.

The potential horticultural merits of our native witch-hazels have long been recognized, yet remain underutilized. It is fairly rare to see these species grown in cultivation outside of botanic gardens and arboreta. Several cultivars of these species have been introduced, probably the most commonly seen being *H. vernalis* 'Autumn Embers', named for its noteworthy burgundy red fall foliage. Among the North American species and their variants growing at the Arboretum, there are three cultivars of vernal witch-hazel—'Lombart's Weeping', 'Orange Glow', and 'Sandra'—and one of common witch-hazel, 'Champlin' (synonym 'Champlin's Red').

Witch-hazels of Asia

In 1907–1908, as Sargent worked with Bush to describe *Hamamelis vernalis,* E. H. Wilson was collecting living plants and seeds of Chinese witch-hazel (*H. mollis*) in central China under the sponsorship of the Arboretum. Wilson wrote of his explorations:

> April 21, 1907
>
> Dear Professor Sargent,
>
> … I visited a part of the mountainous region to the West-south-west of Ichang [Yichang], a part where I had not previously been. Reaching an altitude of about 7,000 feet, the woods in the mts. were still as dormant as in mid-winter, and the snow was still lying in the crevices. In the ravines & open valleys vegetation was advancing, and I made a collection of about 180 species of trees and shrubs … Of shrubs, in the Mt. *Hamamelis mollis* was the most striking with its wealth of yellow flowers, on the low hills. *Loropetalum chinensis* [another member of the family] was a sight for the Gods …
>
> With kindest regards,
>
> I am, Dear Professor,
>
> Faithfully and obediently yours,
>
> E. H. Wilson

Although still quite underutilized in our cultivated landscapes, the Asian witch-hazels and their hybrids have certainly received greater horticultural attention. Chinese witch-hazel is the least hardy of the species but is also the showiest, with bright yellow petals and red calyx-lobes, and fragrance well beyond the others. The previous season's leaves on *H. mollis* can be persistent, appearing dried out, brown, and obscuring the blooms even in late winter.

ANDREW GAPINSKI

This cultivar of Chinese witch-hazel (*Hamamelis mollis* 'Brevipetala') shows the species' trait of leaf retention.

KYLE PORT

This Japanese witch-hazel variant (*Hamamelis japonica* f. *flavopurpurascens,* accession 621-79-A) is notable for its multi-colored flowers.

It is found growing natively in the forests and thickets of central and eastern China. Japanese witch-hazel (*H. japonica*) differs from Chinese witch-hazel in several ways; it has a more flat-topped form, blooms slightly later, has cold-hardier flower buds, and its flowers have slightly longer and wavier petals but are often produced less abundantly and are muted in color. As the name suggests, *H. japonica* is endemic to Japan. The fall foliage color of both species can be quite spectacular.

Sargent himself collected seed of Japanese witch-hazel in 1892 as he explored the island's flora. He wrote observations of the encounter in his 1894 publication, *Forest Flora of Japan*:

> The Japanese *Hamamelis* … is already an inhabitant of our gardens, where, unlike the American species which flowers in the autumn, it produces its orange or wine-colored flowers in March [*H. vernalis* had not yet been described]. *Hamamelis japonica* is one of the common forest-shrubs or small trees in its native country, where specimens occasionally occur thirty or forty feet in height, with stout straight trunks and broad shapely heads. In autumn the leaves turn bright clear yellow; but on one form which we found on Mount Hakkoda, near Aomori, with small thick often rounded leaves (*Hamamelis arborescens* of Hort., Veitch), they were conspicuous from their deep rich vinous red color. This may, perhaps, prove to be a second Japanese species.

As Sargent's observations in the wild suggest, the fall color can be quite variable, with combinations ranging from yellow to purple. None of the witch-hazel representatives from Sargent's 1892 voyage remain in the collections today, but a rather stately, vase-shaped specimen of *H. japonica* (accession 475-90-A) can be found growing in the Leventritt Shrub and Vine Garden.

As well, while none of the witch-hazels Wilson collected directly for the Arboretum remain in our collections today, the lineage of his 1907–1908 voyage lives on in a very significant way. On February 21, 1908, Wilson wrote Sargent detailing the contents of cases of plant material that he was sending to the Arboretum, and explained: "The uncertainty regarding the arrival of these plants in a living state makes


specimen designated in
the description
× Hamamelis intermedia
Rehd.
HERBARIUM OF THE ARNOLD ARBORETUM
HARVARD UNIVERSITY
Hamamelis mollis Oliver
Seed, from #14691, Arb., 1928
Flowers with center and base of
petals red-brown
Cult. Arboretum. #1173-28-F
Coll. E. J. P. March 20, 1936
HERBARIUM
OF THE
ARNOLD ARBORETUM
HARVARD UNIVERSITY
THE HARVARD UNIVERSITY HERBARIA
00043445
copyright reserved
cm

ARNOLD ARBORETUM

Flowers of *Hamamelis × intermedia* 'Arnold Promise' (accession 195-2005-A).

one anxious. Should fortune favor us and they arrive in a satisfactory condition you will possess many plants of more than ordinary interest and which are worth much from the scientific and arboricultural standpoint. If it fails we must try again on other lines." Two months later the cases did arrive, but the contents were in poor condition as he feared. Of the news, Wilson wrote "I need not enter into my feeling of bitter disappointment and vexation … In slang language I was knocked all of a heap." Although the mortality in Wilson's early shipments to the Arboretum may have been high, some material did survive the journey. Among the survivors were seeds from *H. mollis* collected in Changyang Hsien, Hubei, under Wilson Collection Number 624, later becoming Arboretum accession 14691.

After accession 14691 had grown in the collections for a number of years, William Judd, propagator at the time, collected open-pollinated seed from this remarkable specimen of Chinese witch-hazel in 1928. The plant was growing in close proximity to other witch-hazels in the Arboretum's collections. Germinated the following spring, seven of the seedlings would eventually be planted in the collections carrying with them accession number 1173-28. Two of these original seedlings (1173-28-A and G) can still be found growing on the grounds today. In the years that followed, these plants were under careful observation, as several herbarium vouchers from the mid-1930s in the Harvard University Herbaria attest. Through such observations, it was determined that the open-pollinated nature by which the seeds were produced led to none of the seedlings being true *H. mollis,* but that they were in fact hybrids between *H. mollis* and *H. japonica,* displaying traits of both parent species. In 1945, Rehder named the hybrid *Hamamelis × intermedia,* given the "intermediate" traits of the parents exhibited in the new hybrid.

The Best of All in Flower

> Witch-hazels seem to be the true harbingers of spring … However the Japanese witch-hazel has not proven an outstanding plant in bloom because the flowers are not profusely borne and mixed in color with some red, which detracts from the brilliance of the color display in early spring. On the other hand, the Chinese witch-hazel, long noted as a good and fragrant blooming plant, has proved disappointing many years in the Arnold Arboretum because the flower buds have been killed by cold winter.
>
> Donald Wyman, 1963

One of the Judd hybrid seedlings (accession 1173-28-B) had been planted beside the Hunnewell Building, and as it grew it was noted as exceptional among its siblings. In a plant records entry from March 24, 1959, Arboretum

Herbarium voucher taken March 20, 1936, by Ernest Jesse Palmer of one of the plants (1173-28-F) started from seeds of accession 14691 in 1928 by William Judd. Note that the original collection description was that of *Hamamelis mollis,* which was subsequently revised to read "× *Hamamelis intermedia* Rehd." once it was determined that the 1173-28 plants were in fact open-pollinated hybrids of *H. mollis* and *H. japonica.* Of this particular hybrid plant (1173-28-F), Donald Wyman noted in 1959 that it was "more japonica type" in reference to the traits typical of the hybrid's paternal parent (Japanese witch-hazel), including longer petals, an observation that can be seen in this voucher.

KYLE PORT

The specimen of 'Arnold Promise' witch-hazel (accession 396-69-A) that grows near the Hunnewell Building, seen in full flower during a snowstorm on March 8, 2013.

horticulturist Donald Wyman referred to it as the "best of all in flower." It captured all of the best floral traits of its maternal parent (*H. mollis*) with profusely borne, fragrant, bold yellow blossoms, as well as desirable characteristics of *H. japonica,* including better winter hardiness, larger petals, and less leaf retention through the winter. It also displayed signs of hybrid vigor, with a more upright form compared to its spreading parents. In the October 25, 1963, issue of *Arnoldia,* Wyman announced that a new clonal cultivar had been registered: *Hamamelis* × *intermedia* 'Arnold Promise'. He compared the plant to an "old friend," which could be observed out the windows of the library and herbarium and was known for its performance and counted on because it had been there a long time, yet was not "unusual" to the people who got used to enjoying it on a continuous basis. Only after several well-traveled visitors called special attention to the specimen was the plant considered for introduction. Although the original plant no longer graces the Hunnewell Building, a cutting taken from it in 1969 (accession 396-69-A) was grown out and planted near the original location in 1979. It survived a temporary relocation to the nursery in 1992 during the renovation of the Hunnewell Building and in 1995 it was returned to the same spot where it still thrives today. Though there are now

A handsome specimen of *Hamamelis mollis* 'Princeton Gold' (accession 338-2002-A) blooms at the edge of the Arboretum's Leventritt Shrub and Vine Garden.

ANDREW GAPINSKI

'Diane' is a *Hamamelis* × *intermedia* cultivar selected for its carmine flowers.

a great number of *H.* × *intermedia* cultivars that have been introduced to the horticultural industry, 'Arnold Promise' remains among the leaders in the garden world.

Along with the species accessions, the Arboretum's Asian witch-hazel holdings include a number of introduced cultivars. There are currently three Chinese witch-hazel cultivars in the collections: 'Brevipetala', 'Pallida', and 'Princeton Gold'. And in addition to the 14 'Arnold Promise' specimens that adorn the grounds, six other cultivars of *H.* × *intermedia* can be found throughout the landscape, including yellow-petaled 'Moonlight' and five others selected for their unique petal coloration in varying hues of red and orange: 'Diane', 'Feuerzauber', 'Hiltingbury', 'Jelena', and 'Ruby Glow'.

Continuing a Legacy of Discovery

Collection, evaluation, and scientific study of witch-hazels continues at the Arboretum. An accession of particular interest and value is a Chinese witch-hazel that was wild-collected in Wudang Shan, Hubei, China, as part of the 1994 North America–China Plant Exploration Consortium (NACPEC) expedition. One of the expedition's goals was to collect farther north in Hubei than Wilson ever had, with the hope of bringing hardier material into cultivation. The trip's

MICHAEL DOSMANN

The showy flowers of *Hamamelis mollis* accession 698-94-A, wild collected in China.

plant explorers, including former Arboretum Senior Research Scientist Peter Del Tredici, describe their discovery of a witch-hazel grove in fruit: "A little way beyond the *Zelkova* shrine, we found several plants of Chinese witch hazel … loaded with unopened seed capsules. We were particularly pleased to collect this winter-blooming species, which has been gaining popularity in American gardens. After seeing so many plants without seed, it was a treat to find one in fruit, and we greedily collected every seed capsule we could find. The plants were growing on a dry, shady hillside near another plant in the witch hazel family, *Sinowilsonia henryi* …" Two individuals from this collection (697-94-A and 698-94-A) can be found growing on either side of Meadow Road adjacent to the maple collection.

These and other *Hamamelis mollis* specimens are currently part of an investigation by Jessica Savage, a Putnam Fellow at the Arboretum, examining what allows Chinese witch-hazel and other precocious flowering plants to produce flowers early in the year before they develop new leaves. Plants that flower later in the season can use resources provided by their leaves to support their floral displays, but precocious flowering plants depend on nutrients stored in their stems. Her research will help us understand how plants like witch-hazel access the resources required for blooming and overcome the challenges of flowering, in some cases, while the ground is still frozen.

As I write this passage, Michael Dosmann, the Arboretum's Curator of Living Collections, is on an expedition in the Ozarks with several botanical colleagues. *Hamamelis vernalis* is on the group's list of targeted species for collection. The seeds and stories he brings back from his journey will most certainly add to the rich history of witch-hazel at the Arboretum and deepen our understanding of this exceptional genus.

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Did American Chestnut Really Dominate the Eastern Forest?

Edward K. Faison and David R. Foster

"The American chestnut once comprised 25% or more of the Native Eastern Hardwood Forest." ***American Scientist*** **(1988)**

"Chestnut was perhaps the most widespread and abundant species in the Eastern United States since the last glaciation." ***USDA Forest Service Southern Research Station General Technical Report General Technical Report SRS-173*** **(2013)**

"Before the turn of the century, the eastern half of the United States was dominated by the American chestnut." ***American Chestnut Research and Restoration Project, SUNY College of Environmental Science and Forestry*** **(2013)**

Along with the bison and the passenger pigeon, the American chestnut forms an iconic triumvirate of the grandeur of the American wilderness and the devastation that human activity wrought upon it over the past three centuries. Just as the bison was the preeminent large mammal on the continent and the passenger pigeon the most abundant bird, so is chestnut often described as having dominated the eastern forest (or across its geographic range) prior to its destruction by an introduced Asian chestnut blight.

By all accounts chestnut was a magnificent and invaluable tree. It was among the fastest growing, tallest, and widest-trunked trees in the eastern United States. The strength, straight grain, and decay resistance of its wood made it ideal for framing, finished lumber, and fencing, and its regular production of nuts provided abundant food for native and European peoples, domestic livestock, and diverse wildlife. But was it really the dominant tree in the eastern forest?

Dominant species, in the words of forest ecologist E. Lucy Braun, are "those trees of the canopy, or superior arboreal layer, which numerically predominate." Given American chestnut's purported prior dominance in the eastern deciduous forest, we would expect the tree to have ranged widely across the East relative to other common tree species and to occupy a superior place in written accounts by early naturalists and explorers, early land survey records, forest surveys of the early twentieth century, and the paleoecological record. In fact, these sources reveal a very different story.

Accounts by Early Explorers and Naturalists

Accounts by foresters about chestnut's abundance at the turn of the twentieth century have been widely cited in the scientific and popular literature as evidence of the tree's former dominance. Descriptions of chestnut by naturalists and explorers at the time of European settlement, on the other hand, are rarely cited. Early written records must be used with caution, given that they were often written by non-botanists and provide a potentially biased assessment of previous forest conditions (Whitney 1994). Nonetheless, these descriptions—particularly if they correspond with other available lines of evidence—provide valuable eyewitness accounts of eastern forests prior to their widespread modification by Euro-

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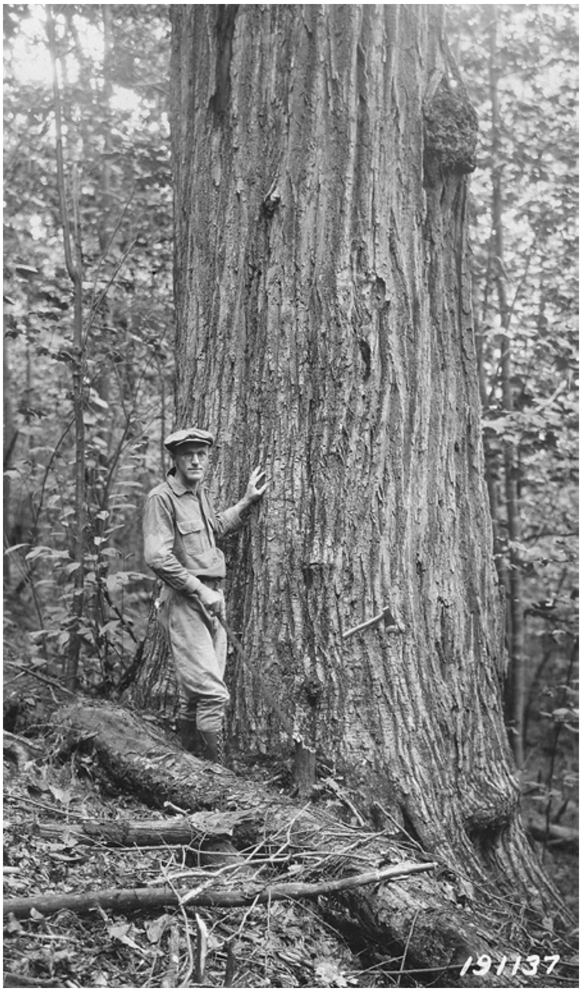


DAVID R. FOSTER

(Left) A large American chestnut photographed in the Monongahela National Forest, West Virginia, in 1923. (Right) Foliage of American chestnut (*Castanea dentata*).

pean settlement. Below are selected quotations that reference chestnut and other species by some of the more important early explorers and naturalists in the Eastern United States.

John Smith, New England coast (early 1600s): "Oke [oak], is the chiefe wood, of which there is great difference in regard of the soil where it groweth; fir, pine, walnut, chestnut, birch, ash, elm …, and many other sorts." (Smith 1616)

Colonel William Byrd, Virginia (1737): "chestnut trees grow very tall and thick, mostly, however, in mountainous regions and high land …" (Bolgiano and Novak 2007)

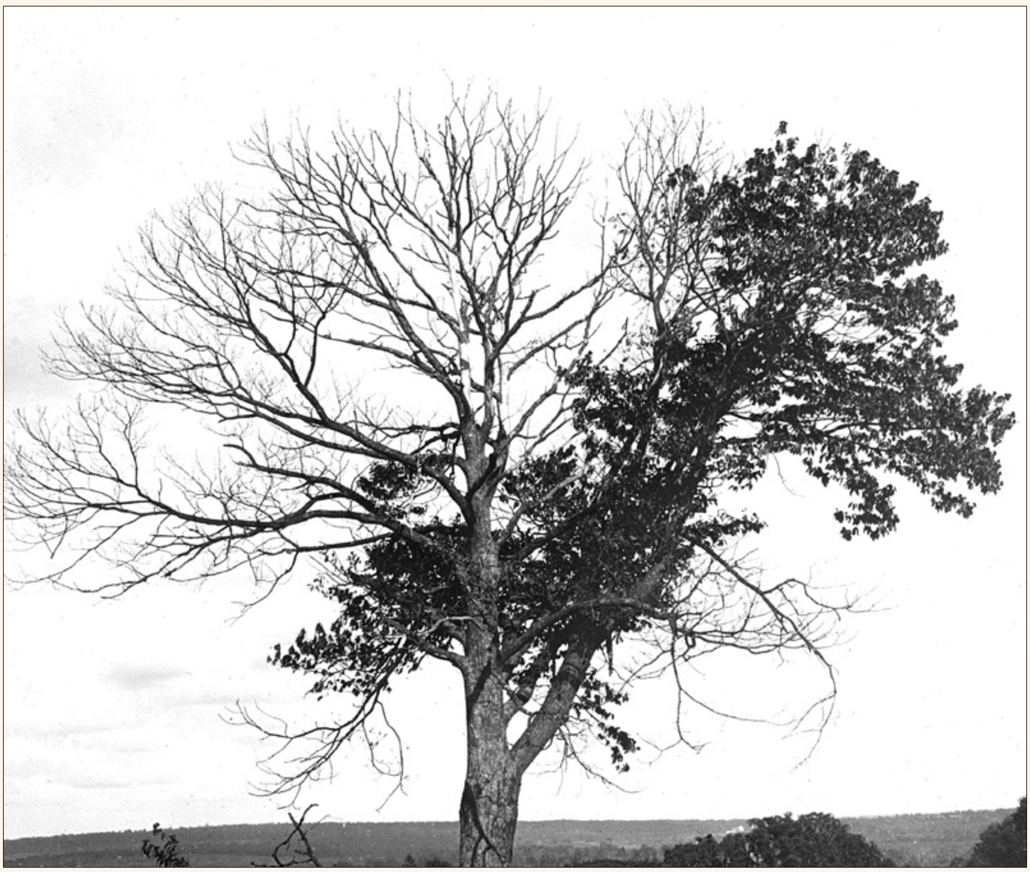
William Bartram, northern Alabama–Mississippi border (late eighteenth century): "[we entered] a vast open forest which continued for above seventy miles … without any considerable variation … the forests consist chiefly of Oak, Hiccory, Ash, Sour Gum, Sweet Gum, Beech, Mulberry, Scarlet maple, Black Walnut, Dogwood, *Aesculus pavia, Prunus indica,* Ptelea, and an abundance of chestnut on the hills, with *Pinus taeda* and *Pinus lutea.*" (Bartram 1976)

Although these accounts represent only a very small sample of early observations, they offer some general patterns that are reinforced

A KILLER ARRIVES

Chestnut blight (*Cryphonectria parasitica*) was first discovered in 1904 in a stand of American chestnuts (*Castanea dentata*) in New York's Bronx Zoological Park, perhaps arriving on imported nursery stock of *Castanea crenata* from Japan. Subsequent investigation determined that the blight arrived in the late nineteenth century, as evidence suggested that American chestnuts on Long Island had been infected as early as 1893. The effects of the blight were immediate and devastating, often killing mature trees in 2 to 3 years. By 1906, the blight was detected in New Jersey, Maryland, and Virginia and continued to spread rapidly, reaching Pennsylvania in 1908 and North Carolina by 1923. All government efforts to contain or eradicate the blight failed, and ceased entirely by 1915. By the early 1940s the destruction of the American chestnut throughout its 300,000-square-mile range was complete.

The blight spreads by wind-borne fungal spores that invade the tree through cracks or injuries in the bark, killing the cambium and eventually girdling the tree. The roots generally survive the blight, however, and continue to produce sprouts that are eventually killed again before reaching reproductive age. In effect, the chestnut blight converted a once towering overstory tree into an understory shrub.



An American chestnut in Connecticut succumbing to chestnut blight, from the image collection *American Environmental Photographs, 1891–1936,* University of Chicago Library Special Collections.

A large white oak (*Quercus alba*) photographed near New Lenox, Illinois, from the image collection *American Environmental Photographs, 1891–1936,* University of Chicago Library Special Collections.

by many others not reported here, specifically that chestnut appears to have had a relatively restricted niche (mountainous) rather than being generally abundant throughout the landscape, and to have been secondary in importance to oaks (*Quercus*).

The Biogeography of Chestnut

The eastern deciduous forest spans approximately 926,000 square miles in North America, covering 13 entire states and substantial portions of 10 others from Maine to Minnesota and south to Texas and Georgia. This vast area is broadly united by a cover of deciduous or mixed deciduous-coniferous forest, but otherwise is far from uniform. Five climatic regions, twelve geomorphic regions, and five soil regions define this broad area. Climate, landforms, and proximity to the coast determine the frequency and type of natural disturbances (e.g., tornadoes, hurricanes, fires, ice storms) that influence a particular region, as well as the distribution and abundance of human populations and their disturbances such as tree cutting, agriculture, and the removal and introduction of wildlife. The physical environment and its associated natural and human disturbances, in turn, shape the vegetation.

For a tree species to dominate an area as broad and diverse as the eastern forest it needs to be an ecological generalist. Relative to other common species like white oak (*Quercus alba*),

DAVID LEE

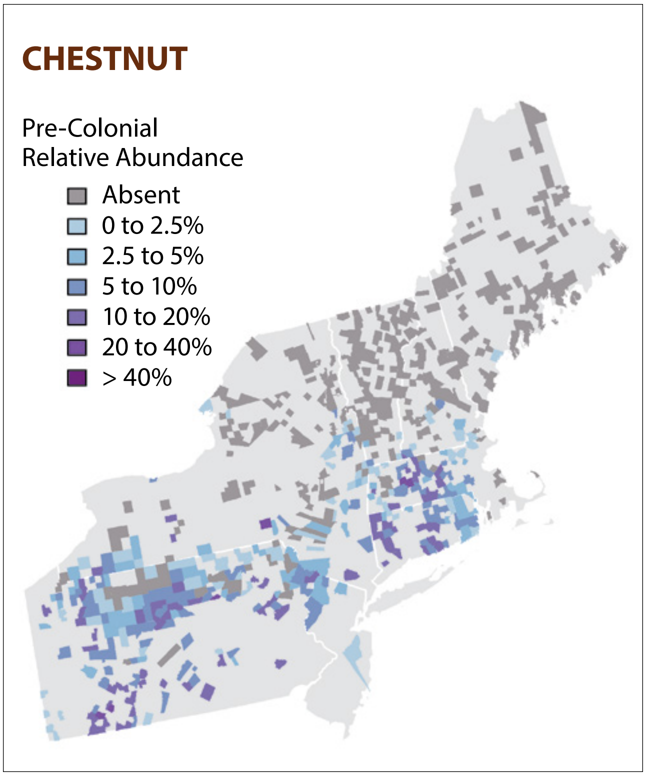
Sugar maple (*Acer saccharum*) leaves in autumn.

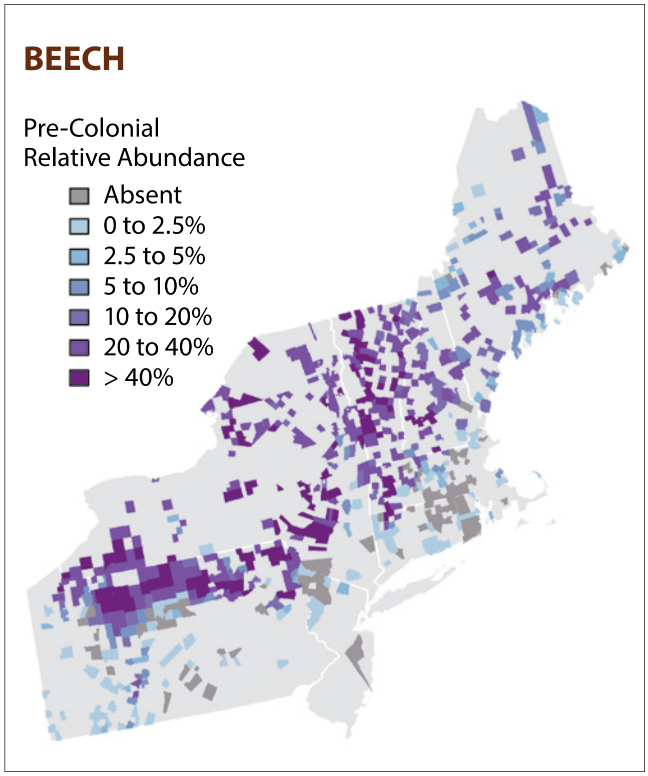
An impressive sugar maple (*Acer saccharum*) photographed near Golf, Illinois, from the image collection *American Environmental Photographs, 1891–1936*, University of Chicago Library Special Collections.

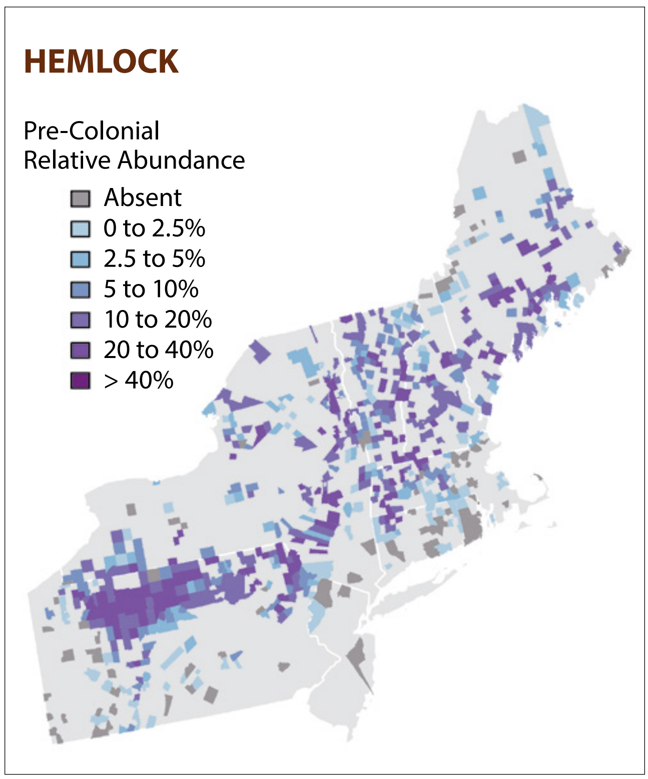
American beech (*Fagus grandifolia*), red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*), chestnut had limited ecological amplitude. Chestnut has high water requirements relative to oaks and is restricted to moderate climates. Hence, it grew predominantly—as the early explorers noted—in sloping topography, particularly on moist, well-drained lower slopes and on some rocky ridges. Chestnut generally fared poorly on sandy coastal plains and outwash soils, clayey soils, saturated wetland soils, or calcium-rich sites. Much of the southeastern coast of the United States is dominated by sandy soils and therefore lacked chestnut altogether. Large areas of the midwestern section of the eastern forest have calcium-rich soils and relatively low rainfall and were thus also unsuitable for chestnut. In northern New England, northern New York, and upper Michigan, extremely cold winters were largely prohibitive to chestnut, which is susceptible to cold and frost damage. In sum, chestnut ranged across only about 309,000 square miles of eastern North America in the early twentieth century—about one-third of the Eastern forest. In contrast, sugar maple, red maple, white oak, red oak (*Quercus rubra*), American beech, and American basswood (*Tilia americana*) all have geographic ranges that exceeded chestnut's by at least a factor of three (Little 1971).

Witness Trees

Early land surveys conducted at the time of European settlement frequently utilized trees, known as witness trees, as corner posts and reference points, and surveyors often recorded each tree to genus or species. Compiled across counties, states, and regions, witness trees offer a formidable inventory of the forest composition that greeted the first European settlers. Early land survey data reveal that chestnut was far less abundant at the time of European settlement than the oft-quoted 25% of the forest. A recent paper by Jonathan Thompson, Charles Cogbill, and colleagues compiled witness tree data from over 700 townships from nine states in the northeastern United States. Their results show that chestnut comprised a mere 3% of trees in the region and never exceeded 25%







American chestnut abundance compared with American beech and eastern hemlock abundance in the Northeast at the time of European settlement as determined by early land survey data (Thompson et al. 2013)

of trees in a single town. In contrast, beech comprised 22% of trees across the region; oaks, predominantly white oak, 17.5%; and hemlock 11%.

Two decades ago, forest historian Gordon Whitney compiled maps of tree species abundance from land survey data across the midwestern United States. Data from about 100 counties or townships across eight states of the upper Midwest reveal that chestnut was never the dominant tree, comprising 5 to 15% of trees in a small section of Ohio and 0 to 4% of trees in the rest of the region. In contrast, beech and especially white oak were frequently the dominant tree, often comprising 25 to 65% of all trees. Limited early land survey data from the southern regions of the eastern forest also portray chestnut as a secondary species. Chest-

Dominant tree species and corresponding abundance and rank of American chestnut at the time of European settlement identified from early land survey data in the southeastern United States. Adapted from Abrams (2003).

Location	Dominant Tree Species and Abundance (%)	Chestnut Abundance (%)	Chestnut Rank	Reference
Eastern West Virginia – Ridge and Valley	White oak (33)	5	5	Abrams and McCay 1996
Eastern West Virginia – Allegheny Mts.	Beech (13)	6	8	Abrams and McCay 1996
Southern West Virginia	White oak (24)	12	2	Abrams et al. 1995
Northern Virginia	White oak (49)	0	NA	Orwig and Abrams 1994
Southwestern Virginia	Red oak (25)	9	3	McCormick and Platt 1980
Western Virginia	White oak (26)	5	5	Stephenson et al. 1992
Central Georgia	Pine, mostly loblolly and shortleaf (27) Post oak (18)	2	9	Cowell 1995
Northeastern Georgia	Pine (26) American chestnut (20)	20	1	Bratton and Meier 1998
Southcentral Tennessee	Post Oak (11)	2	11	DeSelm 1994
Northern Florida	Magnolia (21)	0	NA	Delcourt and Delcourt 1977
Southeastern Texas	Pine, mostly longleaf (25)	0	NA	Schafale and Harcombe 1983
Southeastern Louisiana	Magnolia (13)	0	NA	Delcourt and Delcourt 1974
Northeastern Louisiana	Pine, longleaf, shortleaf, and loblolly (24) White oak (11)	0	NA	Delcourt 1976
Eastern Alabama	Pine, 7 species (44) Post oak (12)	2	9	Black et al. 2002
Southern Arkansas	Black oak (18)	0	NA	Bragg 2003


JOHN S. BURK

A white oak (*Quercus alba*) in New Braintree, Massachusetts.

nut was the first-ranked species in only one of 15 locations, whereas white oak was the first-ranked tree in five of 15 locations (see Table on facing page).

Early Twentieth Century Forest Surveys

E. Lucy Braun conducted and compiled extensive forest surveys and observations across 120 counties of the eastern forest in the early twentieth century. Her data were predominantly gathered from "original" forests and thus fill in gaps in the witness tree studies, particularly in regions such as the Cumberland Mountains of Kentucky and the Blue Ridge Mountains of North Carolina and Tennessee. Although Braun acknowledged her unequal coverage of different regions, her work remains by far the most comprehensive assessment of the eastern deciduous forest, including American chestnut's abundance, at the time of the chestnut blight. Her surveys and data tables reveal that chestnut was a tree of surprisingly limited dominance. Chestnut was dominant (the most abundant canopy tree) in at least one survey in only 15 of the 120 counties (12.5%) sampled by Braun and others. Sugar maple, white oak, and hemlock were all dominant species in over 20% of the counties sampled, and beech was a dominant tree in over 40% of the counties sampled. In fact, Braun's data suggest that chestnut was not even the most abundant tree within its own geographic range: beech was a dominant species in at least one survey in almost half (48%) of the counties sampled in chestnut's range, whereas chestnut was a dominant tree in less than a quarter (23%) of the counties sampled.

American chestnut was spectacularly abundant in some locations. On north slopes in Joyce

Kilmer Memorial Forest in North Carolina, for instance, it comprised over 83% of the canopy trees, and on the slopes of Salt Pond Mountain in western Virginia, it made up 56 to 85% of the canopy trees (Braun 1950). Chestnut could also grow to enormous size. In a forest in Central Kentucky, Braun wrote that chestnuts, which comprised 22% of the canopy trees, were "by far the largest trees, about 5 feet d.b.h. (diameter at breast height)." But chestnut was far from the only tree to achieve such local dominance; beech, hemlock, sugar maple and white oak all achieved comparable abundances in other stand locations. In 1876, forester A. R. Crandall wrote the following in eastern Kentucky: "white oak has a wider range and greater development in numbers than any other species. In size it ranks with the largest of the hardwood trees …"

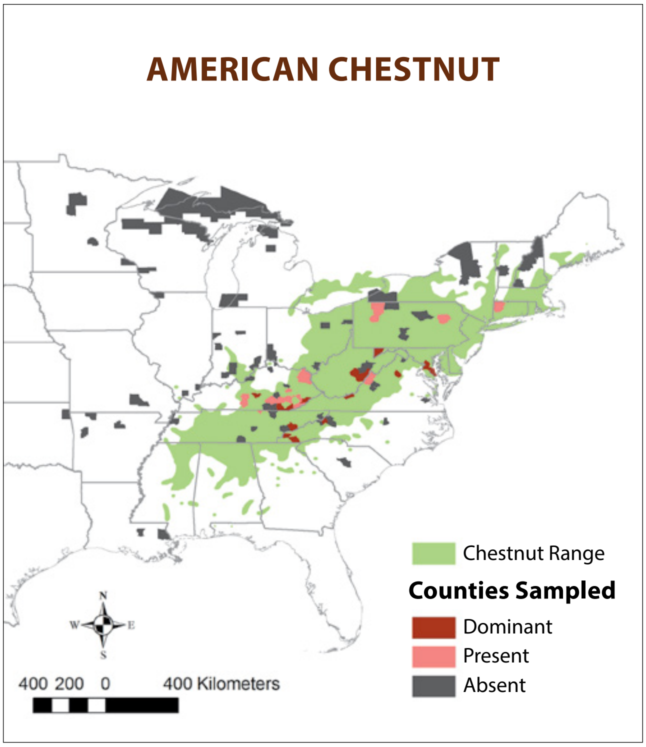
The Rise of Nineteenth Century Logging and Chestnut

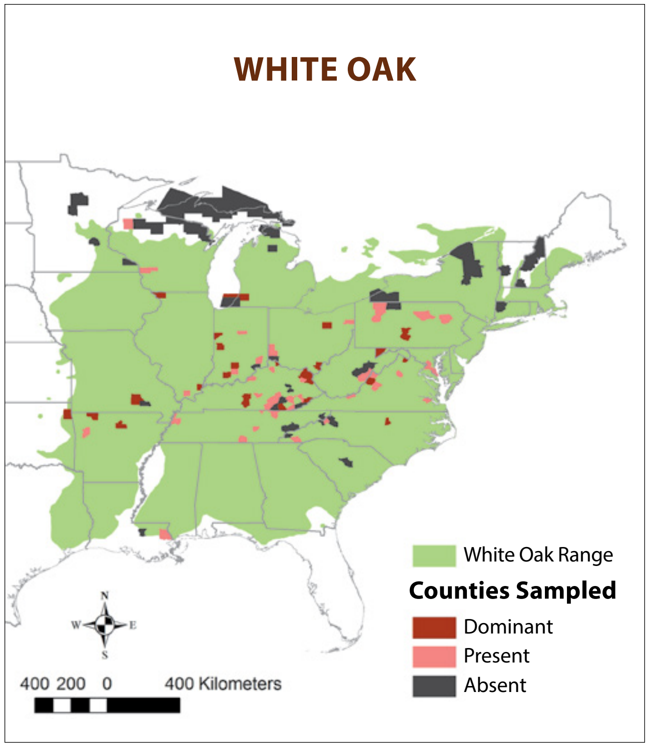
In its destructiveness and lack of legal control, nineteenth century commercial logging was similar to the unrestricted hunting that decimated the passenger pigeon and the bison. However, in an ironic twist to the story of American chestnut, this particular act of exploitation actually promoted chestnut to dominance in parts of its range where it hadn't been dominant before. Chestnut's remarkable

HARVARD FOREST ARCHIVES, HARVARD UNIVERSITY

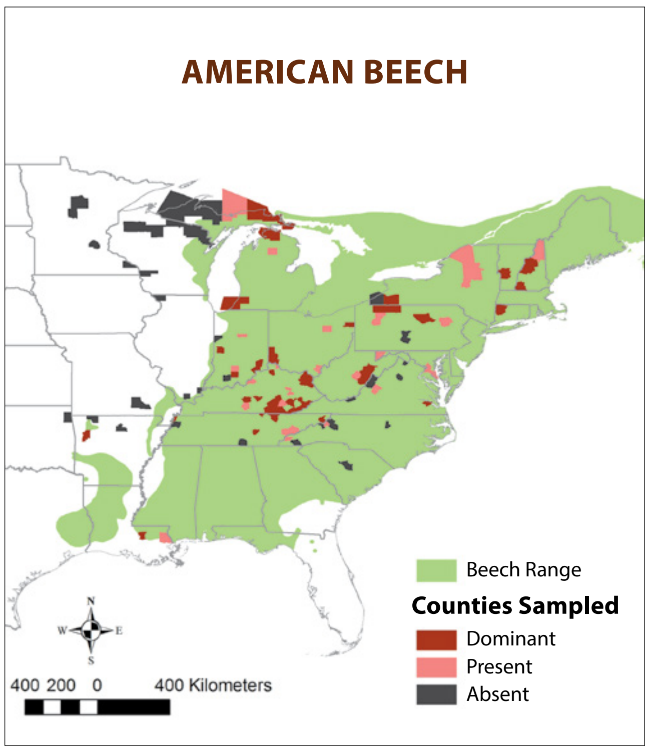
A stand of American beech (*Fagus grandifolia*) in Harvard Forest's Pisgah Tract in New Hampshire, April 1930.

A ring of new shoots growing around the cut stump of an American chestnut, from the image collection *American Environmental Photographs, 1891–1936,* University of Chicago Library Special Collections.





American chestnut's geographic range and extent of dominance compared to that of white oak and American beech in the early twentieth century. Data compiled by Braun (1950).



ability to sprout vigorously from cut stumps, including those of large diameter and advanced age, made it better adapted to intensive logging than any other hardwood tree including oaks. As the early Connecticut foresters Hawley and Hawes (1912) wrote, "this sprouting capacity of the species is its strongest characteristic and the one by which with each successive cutting it gains in the struggle for existence with the rival inmates of the woodlot." Interestingly, chestnut's sprouting capacity was much more prominent in the Northeast than in the southern parts of chestnut's range. In heavily cutover forests of northern New Jersey and southern New England, chestnut increased from 5 to 15% of the forest during the early colonial period to an estimated 50% of the standing timber in Connecticut. Because Braun focused

A stand of American chestnut in Big Creek Gap, Tennessee, from the image collection *American Environmental Photographs, 1891–1936,* University of Chicago Library Special Collections.

on "original" forests in her surveys, she largely avoided surveying the cutover southern New England region so her data probably underestimate chestnut's abundance in the Northeast. But it's important to remember that southern New England represents a small fraction of chestnut's range and the eastern forest overall.

The Last to Arrive: Chestnut Since the Last Ice Age

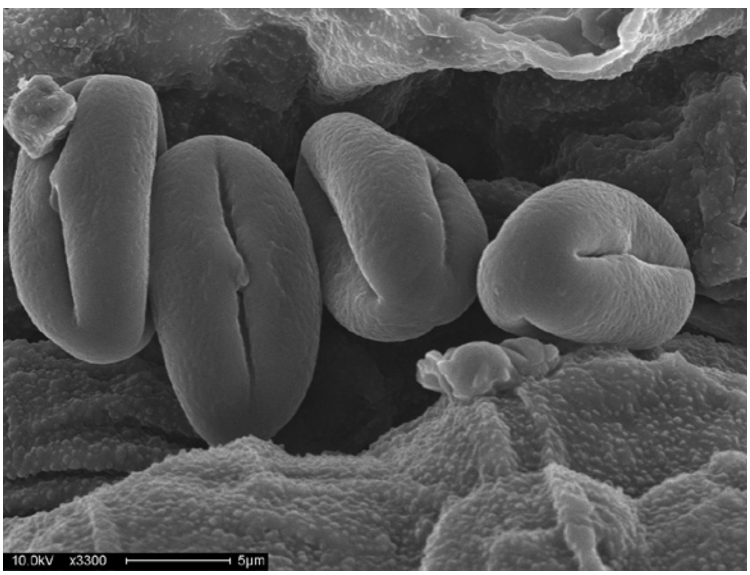
Fossil pollen records in the Eastern forest enable reconstruction of vegetation communities and tree species that have dominated forests over the past 15,000 to 50,000 years. In formerly glaciated areas such as the Northeast, pollen records provide a chronological record of recolonization of forest vegetation after glacial melt some 15,000 to 20,000 years BP (before present). In southern New England, ash (*Fraxinus*), birch (*Betula*), ironwood (both *Ostrya* and *Carpinus,* whose pollens are indistinguishable from each other), and oak arrived first, followed by maples; deciduous forests replaced coniferous forests about 9,000 years BP. Beech arrived about 8,000 years BP, and hickory about 6,000 years BP. Not until about 2,000 years BP does chestnut pollen appear in the sediment record, earning chestnut the distinction of being the last major tree species to recolonize the region after deglaciation (Davis 1983). When chestnut finally does appear in the sediment record, it generally doesn't exceed about 4 to 7% of the pollen types across the region with the exception of one record in northwestern Connecticut where it reaches 18 to 19% (Paillet 1991, Oswald et al. 2007). In contrast, oak pollen consistently comprises 40 to 60% of the pollen and beech 5 to 20%. Interestingly, chestnut does achieve great dominance (40 to 70%) at the stand scale in a few local New England pollen records (Foster et al. 1992, 2002), exemplifying the importance of spatial scale when considering the abundance of this species.

What accounts for chestnut's late arrival to New England? One possible reason is that the climate of the Northeast throughout much of the Holocene was too dry for chestnut. Other researchers have posited a lack of favorable well-drained germination sites in southern New England after deglaciation, or too much lime in the soil that took millennia to leach away. Chestnut is also self-sterile unlike many other trees that are self-fertile, and thus the chances of establishing new populations were much lower for this tree. Whether dispersal or environmentally limited, it is clear that

SPATIAL SCALE

Spatial scale refers to the size or extent of the area under consideration. A stand is a relatively small area of forest that is spatially continuous in structure and composition and is exposed to similar soil and climatic conditions. In paleoecology the size of the catch basin (e.g., lake, pond, swamp, or small hollow) determines the distance from which pollen in the sediments originates. Sediments from a small forest hollow will contain pollen from vegetation growing predominantly in the immediate stand (a "stand scale" investigation), whereas sediments from a large lake are dominated by pollen from the broader landscape up to 20 miles away.

DANILO D. FERNANDO, SUNY-ESF



A micrograph of American chestnut pollen.

chestnut was poorly adapted to recolonizing the deglaciated Northeast compared to other hardwood trees.

Chestnut had a much longer history in the unglaciated Southeast. Chestnut pollen appears in the pollen record as early as 16,000 years BP in Tennessee (Davis 1983). Although a few records show chestnut to be dominant or co-dominant with oaks during the Holocene in the North Carolina and Tennessee mountains, most of the records from the southern and central Appalachians analyzed by William Watts, Paul and Hazel Delcourt, and others reveal oaks to be dominant over chestnut. Still, comparisons between oak and chestnut pollen abundance should be undertaken with caution. Oak pollen grains are indistinguishable among species, and many are therefore combined into a single category of "oak" pollen. Chestnut, on the other hand, is the only species in its genus in the Northeast and is one of two species (the other is dwarf chinkapin, *Castanea pumila*) in the central and southern Appalachians. Oak pollen is wind dispersed and therefore is generally produced in larger quantities than is chestnut pollen, which is partially dispersed by insects. Hence, chestnut pollen is generally underrepresented in the pollen record, relative to oaks. Still, chestnut's relatively minor status in the pollen record is consistent with its secondary status in the witness tree data and in accounts by early settlers. In addition,

MISSOURI BOTANICAL GARDEN, WWW.BOTANICUS.ORG

An illustration of dwarf chinkapin (*Castanea pumila*) from Mark Catesby's *The Natural History of Carolina, Florida, and the Bahama Islands, Volume 1.* This etching was first published in 1729.

chestnut's great abundance (40 to 45%) in a few southern Appalachian pollen records analyzed by the Delcourts and stand-level records from Massachusetts are consistent with twentieth century forest surveys in which chestnut achieved great dominance in some landscapes and topographic positions, but generally not at broader scales.

Concluding Thoughts

American chestnut was once a common tree species throughout its Appalachian Mountain range and a dominant species in parts of its central and southern range (primarily the oak-chestnut forest region). However, prior to European settlement, it was less dominant than white oak and beech and far less widespread than most other major tree species. With increasing timber harvesting in the nineteenth and early twentieth centuries, chestnut's dominance increased in the northern part of its range in heavily cut-over forestland. Still, the tree remained absent from fully two-thirds of the eastern forest, precluding it from ever being the dominant tree of this biome.

Revealing the truth about American chestnut's relatively limited place in the Eastern forest does not diminish the grandeur of this great tree, its historical importance to cultures of the central and southern Appalachians, and the great tragedy of its demise. Chestnut remains the flagship example of the potential dangers posed by introduced pathogens in our native forests. But we should be careful not to let a great tragedy and impassioned restoration efforts trump the available data when discussing the history of this tree.

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Reading Tree Roots for Clues: The Habits of Truffles and Other Ectomycorrhizal Cup Fungi

Rosanne Healy

Here's something to ponder: The health and regeneration of grand old oaks (*Quercus*) and majestic pines (*Pinus*) is dependent on the well-being of tiny fungi that associate with the trees' roots. Such small organisms have a big role to play not only for oaks and pines but also for many other trees that rely on their fungal partners to get them through lean and dry times. An estimated 86% of plant species benefit from (or are even dependent on) fungal root associates that transfer water and nutrients to the plant in exchange for carbohydrates (Brundrett 2009). Carbohydrates from plants are the result of atmospheric CO_2 (carbon dioxide) fixation through photosynthesis and subsequent processes, which the fungi are incapable of doing.

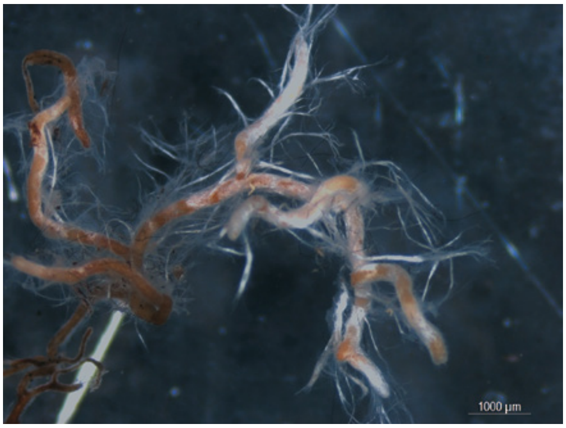
The fungal root associates are the mycorrhizal (myco=fungus, rhiza=root) fungi. They can be roughly sorted into two types based on how they associate with the roots. One type is mostly invisible to us because their hyphae are inside the root (endomycorrhizae), and the other can be seen as a mantle surrounding the root tip (ectomycorrhizae). The endomycorrhizal fungi are root associates of the vast majority of herbaceous plants and certain tree species. This article focuses on ectomycorrhizal fungi, which grow mostly in association with trees rather than herbaceous plants. They make their presence known to us not only because we can see them on tree roots but also because we see their fruiting bodies, particularly from midsummer into fall here in New England.

NANCY ROSE

Trees such as the red oaks (*Quercus rubra*) and eastern white pines (*Pinus strobus*) seen here benefit from ectomycorrhizal fungi.

ALL IMAGES BY THE AUTHOR EXCEPT WHERE NOTED

The color and "furry" appearance of this ectomycorrhizal red oak root tip are from the fungal symbiont, a *Scleroderma* fungus.



The ectomycorrhizal root tips (top) and fruiting bodies (bottom, at several stages of maturity) of the basidiomycete fungus *Cortinarius armillatus.*

Which fungi are they?

Thanks to ever more ingenious methods of molecular fingerprinting of fungi, and a growing database of DNA sequences for fungi of all kinds, we now know much more about what species are involved in these relationships. The ectomycorrhizal fungi include some of the largest and most colorful of the fleshy basidiomycete fungi like *Cortinarius* and *Russula,* as well as prized edibles like the king bolete and chanterelle, and deadly poisonous species such as the death cap, *Amanita phalloides.* Far less is known about the cup fungi that form ectomycorrhizae, despite their long history of study.

The term "mycorrhiza" was coined by botanist Albert Frank in 1885 while he studied the relationship of *Tuber,* a truffle cup fungus, with its host tree roots in order to determine how to cultivate this gastronomically important fungus. He and his student, Albert Schlicht, discovered that the majority of apparently healthy plants that they surveyed in Germany had fungal root associates. Frank was the first to hypothesize that the fungi observed on roots were mutually beneficial with the trees rather than parasitic (Trappe 2005), a hypothesis that has since been borne out by many studies.

Most truffles, including the economically and gastronomically important *Tuber* species that interested Frank, are ectomycorrhizal. I have been studying *Pachyphlodes,* a common but generally ignored truffle genus, for the past 15 years. During these studies I collaborated with Harvard University Herbaria cup fungus experts Don Pfister and Matthew Smith (now at the University of Florida). We noticed that the asexual form of truffles, termed sporemats here, occur most abundantly on bare or nearly bare soil. This was consistent with reports that fruiting bodies of ectomycorrhizal Pezizales (the nomenclatural order for cup fungi) tend to occur in disturbed habitats such as dirt paths or roads in the forest (Petersen 1985). I am now working with Don Pfister to test the hypothesis that ectomycorrhizal Pezizales are more prevalent in managed rather than natural environments. To do this, we are comparing the ectomycorrhizal fungi on roots of red oaks (*Quercus rubra*) in the Arnold Arboretum with those on red oaks in Harvard Forest.

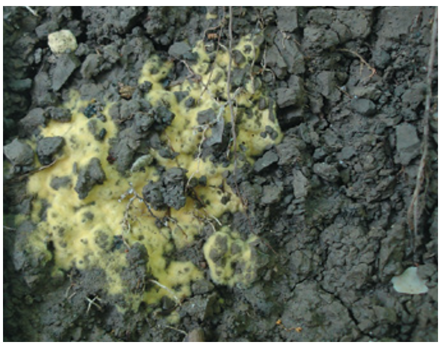
A Tale of Two Sites

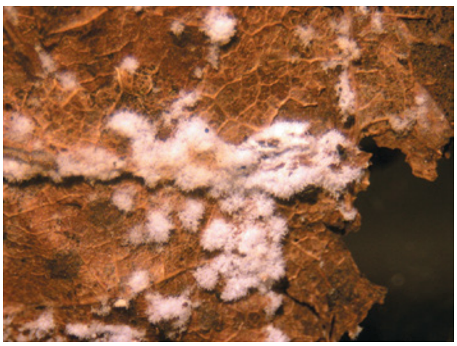
Why choose these two sites for this study? There are some important differences between the Arboretum and the Harvard Forest. The Arboretum habitat is more like a residential area, where much of the understory is kept clear of non-cultivated plant life and the grass is kept short. The soil organic layer is comparatively shallow, and there is not much variety in the litter layer.

In contrast, the forests here in New England are characterized by an understory of regenerat-

RICHARD SCHULHOF

Research indicates that the ample foot paths, mowed lawns, and sparse understory in the Arnold Arboretum will favor Pezizales fungi on the root tips of the ectomycorrhizal trees.





Sporemats of truffle fungi *Pachyphlodes* sp. nov. (left) and *Tuber* sp. nov. (right).

An example of a sporemat and the truffle (*Pachyphlodes ligericus*) that its fungal barcoding sequence matches.

ing trees, native shrubs, vines, and herbs. The ground under the trees is covered by woody and leafy litter, and under that layer is a deep organic layer composed of roots, soil, and partially broken down organic matter that together form a dense mat that requires a knife to cut through it.

Compared to the forest habitat, there is not much in the Arboretum habitat to obstruct the passive transfer of fungal spores produced on the soil surface to roots and mycelia in or below the organic layer. This is possibly an important feature for the cup fungi because in order to fruit, the hyphae of outcrossing species such as *Tuber* must come in contact with a compatible mating type nucleus in another hypha. This is in contrast to most ectomycorrhizal basidiomycete species that form their mycelia with both nuclei soon after germination of their sexual spores. How do compatible mating types of truffles get together if the mycelia are underground? Perhaps the sporemats on the soil surface play a role in this event. If so, mating may be facilitated in an environment such as that found in the Arboretum over that found in a forest.

Ectomycorrhizal basidiomycete fruiting bodies (top) and their root tips (bottom) from (left to right) *Amanita rubescens, Craterellus fallax,* and *Scleroderma areolatum.*

Let's explore that idea a bit. The sporemats are produced on the soil surface, presumably from the ectomycorrhizal roots below the soil surface. They in turn produce massive numbers of spores that are small, light colored, and thin walled, and therefore probably not designed to function as survival structures. We don't know what their function is, but it makes sense that they might be involved in the mating of truffles and other cup fungi that produce them. With this in mind, as part of the study of ectomycorrhizal communities, we also collected sporemats and fruit bodies in the vicinity of the trees we sampled from.

Fungus Findings

In order to determine what species are on the roots of the trees we sampled, we utilized a technique that yields the nucleotide sequence of the fungus genome from a nuclear region that is known to mutate quickly enough to show differences in nucleotides between species, but not so quickly that they differ much within species. This region of the genome is not a coding region, and therefore, the mutations have no known impact on reproduction. It is called the internal transcribed spacer region (ITS), and is one of the most useful for studying species limits in the fungi. In fact, this region was recently adopted as the first fungal bar code marker in the recently updated International Code of Nomenclature of algae, fungi and plants (McNeill et al. 2011). There is sufficient data from this genome region available in the National Center for Biotechnology Information (NCBI) that are deposited from national and international studies to be able to place most of the sequences from our study within a genus, and in some cases feel confident about the species, or to tell if it is likely an un-named (in NCBI) species. We can also compare our sequences with others in NCBI from a geographic locality perspective, and thus analyze the likely origins of the fungi on the root tips in our study to decide whether they are native or non-native.

While our study is not yet complete, I would like to share several interesting vignettes that have come to light. Basidiomycetes were the most frequently sequenced from the root tips in both habitats with 59 molecular taxonomic

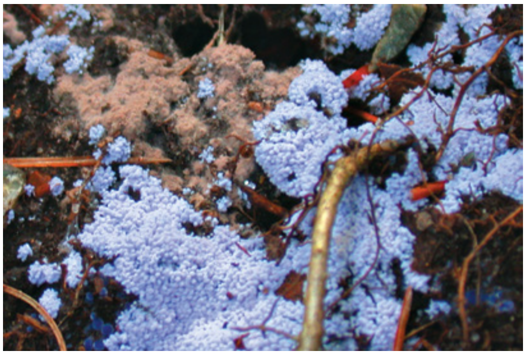
This *Russula* fungus (fruit body and root tip shown) has a sequence that matches root tips in this study, as well as root tips and fruit bodies from a 2006 study by Don Pfister and Sylvia Yang in which they determined that many *Russula* species are exploited by the Indian pipe plant, *Monotropa uniflora.*

units (MOTUs) from Harvard Forest and 56 MOTUs from the Arboretum, 17 of which overlapped in both sites. Some MOTUs could be matched to sequences in GenBank from described species or at least sequenced fruit bodies. *Russula* species were the most frequently sequenced in both habitats with 32 MOTUs. A number of our other sequences matched *Russula* sequences from a previous study by Don Pfister and Sylvia Yang, but not sequences of any described species. A distant second place for most commonly sequenced genus was *Cortinarius* (14 MOTUs) followed by *Lactarius* (9 MOTUs). Even less common (genus followed by MOTUs within parentheses): *Amanita* (4), *Boletus* (1), *Byssocorticium* (1), *Clavulina* (4), *Craterellus* (1), *Entoloma* (3), *Inocybe* (4), *Laccaria* (1), *Piloderma* (1), *Pseudotomentella* (1), *Scleroderma* (2), *Sistotrema* (1), *Strobilomyces* (1), *Tomentella* (7), *Trechispora* (1), and *Tylopilus* (1).

Nearly equal numbers of Ascomycete MOTUs were sequenced from each site. However, there was little overlap in species. It is particularly interesting that the Pezizales had significantly greater species richness and number of root tips in the Arboretum (10 MOTUs) than in the Forest (3 MOTUs). The cup fungi detected on roots in the Arboretum included *Hydnotrya*, four species of *Pachyphlodes*, three species of *Tuber*, and two root tip sequences that have no match to a fruit body sequence. From Harvard

Ectomycorrhizal ascomycete fruiting bodies (above) and their root tips (below) from (left to right) *Elaphomyces muricatus, Pachyphlodes* sp. nov., and *Tuber separans.*

Fruiting bodies of *Leotia lubrica*, commonly known as jelly babies, were found in Harvard Forest.



The researchers sequenced this unusual blue sporemat, which may be *Chromelosporium coerulescens* or a related species.

The distinctive black ectomycorrhiza of a *Cenococcum* fungus.

Forest we detected *Leotia lubrica* (commonly known as jelly babies) and *Elaphomyces* (hart's truffle). Cup fungi detected included *Tuber separans,* and the same species of *Tuber* (species 46) as found in the Arboretum. We also recovered a sequence that matches that of a lovely blue sporemat for which no fruiting body is known. This sporemat may be *Chromelosporium coerulescens* or a close relative. *Cenococcum,* an ascomycete not known to make a fruiting body, but with a very characteristic black ectomycorrhiza was ubiquitous on roots in both habitats.

We collected a number of truffle sporemats on the soil surface in the Arboretum, but in Harvard Forest they were found on top of the leaf litter, and even on the lower trunks of trees. Although we know from other ectomycorrhizal root studies that these species colonize roots, few of their sequences were detected on the roots sampled in this study, and none of their fruiting bodies found. The only evidence of their presence using our sampling technique was their sporemats. This may be because the Pezizales tend to be patchy in their colonization of roots, so they could easily be missed during sampling. The fact that they developed on the surface of the substantial organic layer in the forest shows that the originating mycelium is capable of navigating through the root mat and litter layer from the root tip. Where do the spores from the sporemat go and to what purpose? We don't know. We now see that they are quite capable of being formed atop heavy woodland litter, but we don't know how efficient their dispersal and ultimate journey into the soil is in either a forest or arboretum-like setting.

A second mystery came to light when one of the *Tuber* species detected on roots of a native red oak in the Arboretum was nearly identical in sequence to a species native to Europe, *Tuber borchii.* To our knowledge, this species has never been detected outside of cultivation in North America. Hannah Zurier, a Harvard undergraduate, received a Microbial Sciences Initiative fellowship to (in part) attempt to reconstruct how this truffle came to reside in the Arnold Arboretum. She found the truffle

The fruiting body and root tips of the newly named *Tuber arnoldianum*.

again on the same tree, and is in the process of looking for it on other trees in the vicinity.

A third interesting story involves another *Tuber* species. We detected a species (termed "species 46" by Tuberaceae expert Gregory Bonito, a mycologist at the Royal Botanic Gardens in Melbourne, Australia) on the roots of several trees scattered throughout the Arboretum, as well as from one of the trees sampled in Harvard Forest. Our sequences match those for an undescribed species, known previously only from orchid root tips in New York and red oak root tips from an urban area in New Jersey. We were fortunate to recover some fruiting bodies from the Arboretum so that we will now be able to describe this taxon. The Arnold Arboretum staff has chosen the name *Tuber arnoldianum* for this truffle.

While data are still being gathered, enough has been analyzed at this point (985 root tip sequences from 24 trees in each site) that I expect the pattern of Basidiomycete to Pezizales MOTUs in the two sites to hold up. This pattern continues to support the hypothesis that Pezizales are more prevalent in managed woodland sites such as the Arboretum. We can't be certain of the determining factors for this pattern, but refining the experimental parameters will help to zero in on those factors that are correlative. The well documented history of each accessioned tree, the ease of access to the rich information regarding Arboretum vegetation, and the encouragement and support of research by the staff at the Arnold Arboretum and Harvard Forest make these sites ideal for helping to resolve some of the outstanding questions regarding the ecology of ectomycorrhizal cup fungi.

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The Castor Aralia, *Kalopanax septemlobus*

Kyle Port

Kalopanax is a monotypic genus in Araliaceae, the ginseng family. The lone species, *K. septemlobus,* is a dominant tree in northeastern Asia (Japan, China, Korea, the Russian Far East) where it is valued for the ethnopharmacology of its plant parts and its timber quality. Across Korea, overuse has threatened some wild populations and there are now calls to protect the species.

Castor aralia is a large deciduous tree that can grow to nearly 100 feet (about 30 meters) tall and has an average trunk diameter of about 40 inches (about 100 centimeters). Its stems are armed with stout prickles that yield to thick, deeply furrowed bark with age. It has very large (to 14 inches [36 centimeters] in diameter), long-petioled, 5- to 7-lobed leaves that may turn brilliant greenish yellow in autumn. Castor aralia bears large, wide (to 12 inches [31 centimeters] in diameter) inflorescences with numerous small umbels of white flowers that open in August and September here, providing late season nourishment to an assortment of pollinators. Successful pollination yields abundant blue-black fruits that are retained into winter.

A single castor aralia plant was sent to the Arnold Arboretum in January 1881 by Alphonse Lavallée of Segrez, France. This inaugural specimen was accessioned as *Acanthopanax ricinifolium*—the species' accepted name at the time—and its accession card states only that it was "disposed of" in 1890. Intrigued by its characteristics and determined to cultivate specimens in Boston, Arboretum Director Charles Sprague Sargent collected seeds of the species on his first excursion to Japan in 1892. Two plants hailing from this collection thrive in the Arboretum today. Sargent's account of castor aralia in *Forest Flora of Japan* (1894) inspired additional collections, including J. G. Jack's 1905 seed collections at Lake Chuzenji (Chūzenjiko) and Sapporo, Japan. A total of 27 *Kalopanax septemlobus* accessions are documented in our curated databases and three plants currently grow in the permanent collections.

These handsome specimens grow on the eastern bank of Rehder Pond (accession 841-81-A) and near the paved summit path on Peters Hill (accession 12453-A and C). The younger specimen (841-81-A) was received as a seedling in 1981 from the United States National Arboretum, originating from seeds they received from China's Nanjing Botanical Garden. Growing without competition, its relatively uniform spread of 43 feet (13.1 meters) and height of 35.1 feet (10.7 meters) is remarkable. This specimen is marvelously tactile as the prickles around its 19.6 inch (49.8 centimeter) diameter trunk can still be felt when pressed. The two largest and oldest castor aralias on the grounds are those from Sargent's 1892 collection in Japan. Specimen 12453-A is 52 feet (15.8 meters) tall and has an astoundingly broad spread of 77 feet at its widest point; 12453-C is 34.7 feet (10.6 meters) tall and has a spread of 53 feet (16.1 meters).

In the July 19, 1923, issue of the *Bulletin of Popular Information,* Sargent wrote of castor aralia: "It is one of the most interesting trees in the collection and, because it is so unlike other trees of the northern hemisphere it is often said to resemble a tree of the tropics." The Arnold Arboretum subsequently distributed *Kalopanax septemlobus* seeds and plants to scores of researchers, institutions, nurseries, and hobbyists across the globe. Most prominently, it was among 10 taxa offered as a "reverse birthday present" in celebration of the Arboretum's centennial in 1972 and was included in institutional articles and listings of the best ornamental trees for the New England area.

Enthusiasm for castor aralia has since been tempered, however, as it has shown invasive tendencies in some areas, including the Arboretum grounds. Its fruits are readily consumed—and seeds subsequently dispersed—by birds; the Hokkaido Research Center in Japan documented 27 bird species feeding on *Kalopanax septemlobus* fruits across a 22 acre (9 hectare) site. Recognizing that dispersed seeds germinate in high percentages, we removed 7 accessioned castor aralias between 2010 and 2012. In addition, the practice of culling castor aralia seedlings from natural and cultivated areas of the Arboretum was formalized in our 2011 *Landscape Management Plan.* The conservation of taxa reported to be invasive is a topic of ongoing discussion here and at other botanical institutions. For the time being, don't miss the opportunity to study and marvel at a few of North America's oldest castor aralia here on our grounds.

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