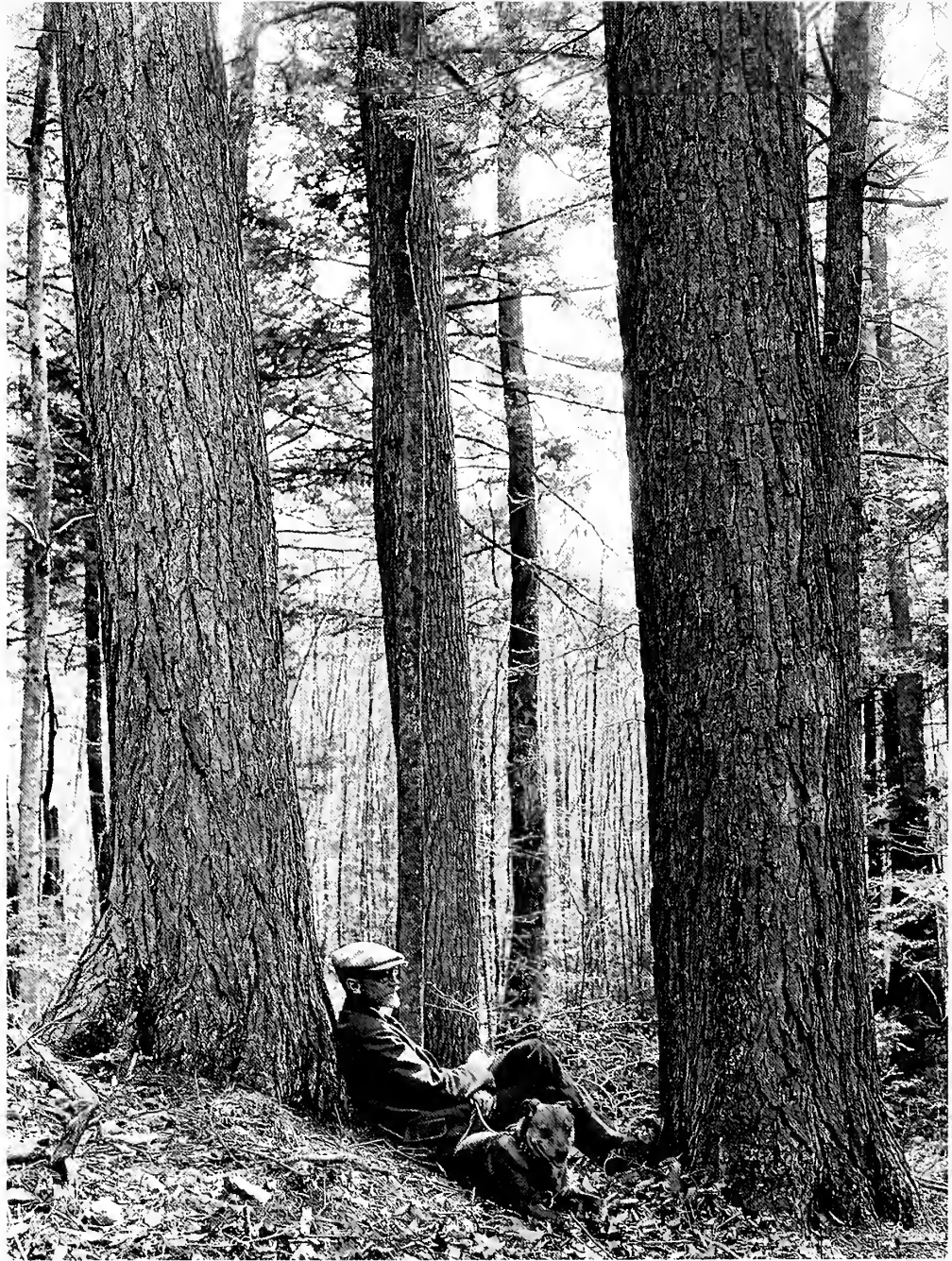


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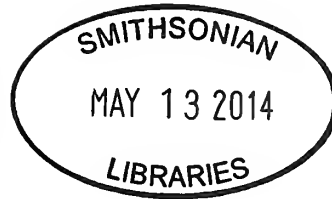




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The Arnold Arboretum
125 Arborway
Boston, MA 02130-3500

Nancy Rose, *Editor*
Andy Winther, *Designer*

Editorial Committee

Phyllis Andersen
Peter Del Tredici
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Kanchi N. Gandhi

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The ARNOLD
ARBORETUM
of HARVARD UNIVERSITY

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Front cover: Glory-of-the-snow (*Chionodoxa* sp.) was in bloom at the foot of an Oriental beech (*Fagus orientalis*, accession 14586-A) on April 9, 2013. Photo by Kyle Port.

Inside front cover: R. T. Fisher, first director of Harvard Forest, and his dog Johnny amid old-growth eastern hemlock and eastern white pine on Harvard Forest's Slab City tract in 1925. Photo courtesy of Harvard Forest Archives.

Inside back cover: *Spiraea prunifolia* var. *simpliciflora* in bloom. Photo by Nancy Rose.

Back cover: A lone specimen of Siberian elm (*Ulmus pumila*) growing by a cultivated field in Hebei, China, photographed by John George Jack on October 4, 1905. Archives of the Arnold Arboretum.

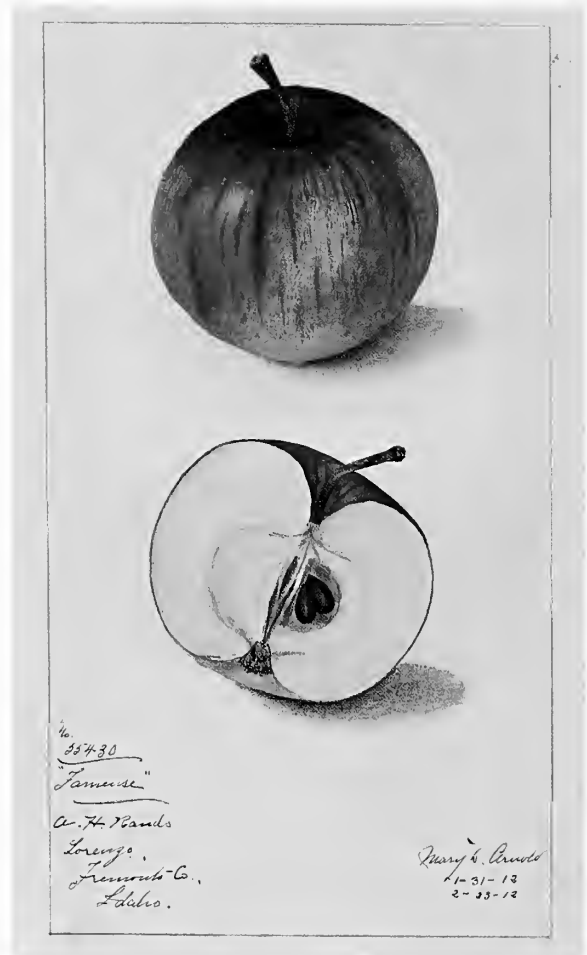
John George Jack: Dendrologist, Educator, Plant Explorer

Lisa Pearson

John George Jack was a notable figure in the early history of the Arnold Arboretum. His story is perhaps less well known than those of his colleagues, but his fifty-year dedication to the study of trees, plant exploration, formal and informal education, and especially the instruction of a generation of Chinese botanists is unmatched. In 2012, the Arboretum was fortunate to acquire a trove of John Jack archival materials from his granddaughter, Constance W. Cross. Included were three manuscripts written by Jack in the early 1940s, in which he gives a lively account of his early life in Canada as well as a detailed look at the beginnings of the Arnold Arboretum. These historical sketches provide new insight on Jack and served as a primary resource for this article.

Roots

John George Jack (1861–1949) was the son and grandson of Scottish immigrants who came in 1832 to Châteauguay, Quebec, then a farming community and now a suburb of Montreal on the south shore of the St. Lawrence River. His grandfather, also named John Jack (1787–1860), was a blacksmith by trade but his father, Robert Jack (1821–1900), instead took up farming on a 150-acre property that stretched from the Châteauguay River to the border with the Caughnawaga First Nations reservation some two miles distant. Early in his career, Robert raised similar crops to his neighbors—potatoes, grain, hay, and livestock—but as time went on he became increasingly interested in experimental fruit growing with an eye to identifying apple varieties that would be productive in Quebec’s challenging climate. His earliest and most successful orchard, planted in 1859 or 1860, was of the cultivar ‘Fameuse’, also known as the “snow apple” for its very white flesh. In effect creating a private agricultural experiment



A watercolor illustration of the apple cultivar ‘Fameuse’ painted by Mary Daisy Arnold in 1912. It is part of the USDA Pomological Watercolor Collection, a group of technically accurate paintings that document fruit and nut varieties developed by growers or introduced by USDA plant explorers around the turn of the twentieth century.

station, he trialed many other types of European apples but they were not sufficiently hardy in that severe northern climate. Robert was also an innovator in growing “boutique” produce for the city market in Montreal, decades ahead of other local farmers. He raised two to three acres of asparagus every year, which provided a welcome influx of much needed cash as well as valuable nutrition for the family at a time of year when it was sorely lacking.

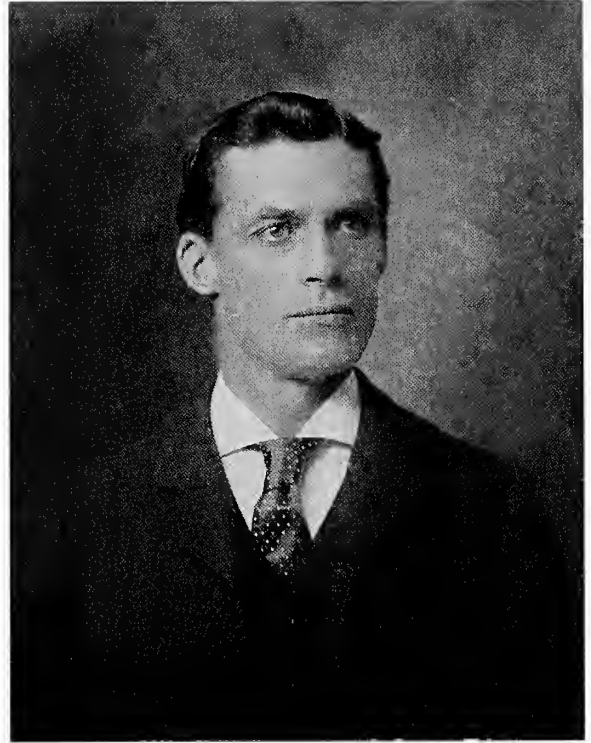
Jack’s mother, Annie Linda Hayr Jack (1839–1912), was born in Northamptonshire, England, and immigrated with her family to the United States in 1852. She was educated at the

Troy Female Seminary in Troy, New York, and taught in the city for several years before moving to Quebec. She had been the teacher at the Protestant school in Châteauguay when she married Robert Jack in June 1860. Annie was a remarkable woman who raised eleven children to adulthood and educated them at home periodically, wrote extensively on gardening and agricultural subjects for the popular press, and kept up a voluminous correspondence.

From a very early age, John Jack was passionately interested in insects. One of his earliest books was the 1862 third edition of Thaddeus William Harris's *A Treatise on Some of the Insects Injurious to Vegetation*, which was his constant guide in the field. He collected specimens in his brief spare time between farm chores and carefully mounted the insects on pins in cigar boxes obtained from tobacconists in Montreal. He later remarked that the lingering tobacco smell probably served as a natural insecticide for his collection. His parents encouraged his collecting, "although they did not have much specific scientific knowledge of insects or plants," he later reminisced. His father, who was liberal-minded when it came to religious exercises, allowed him to spend his Sundays outdoors collecting specimens. Their neighbors came to look upon John Jack as a peculiar child for his single-minded devotion to nature. However, he was vindicated some years later when the Colorado potato beetle infested the region and those same neighbors sought out his extensive knowledge of insect pests. Jack joined the Entomological Society of Ontario when he was just 13 years old. Although the Montreal chapter was small, the dozen or so members gave him great encouragement towards his collecting; through his contacts he was later able to network by mail with entomologists in the United States.

Education

Growing up on a busy farm meant that John Jack's opportunities for formal education were often limited, especially as he grew older and more able to assist his father with the heavy farm work. As a young child he was sent to the local Protestant school with his younger siblings, but on occasion, when their parents



John Jack in March 1898 at age 37, just before his expedition to Pike's Peak.

were in disagreement with the management of the school, all the children were taken out and educated by their mother at home.

Winter was a time when farm work was much reduced, so Jack's parents used that opportunity to send him to boarding schools in the region. Over the winter of 1875–76 he attended the Franklin Academy in Malone, New York, boarding in the home of Mary J. Cantwell, a family friend who was, "a landscape painter of some ability and a woman of liberal ideas and education." According to Jack, it was the longest period of "well ordered" high school education he would ever receive. The next winter he boarded at a private school run by an Episcopal priest. Jack found him "straight-laced" and felt he had not gotten very much out of the experience. After this interlude, his formal education effectively ended, save for some lessons in Latin and Greek that he received from the family's local minister. These lessons became less attractive for Jack when he realized that the clergyman was trying to lead him towards becoming a clergyman himself! His parents had enter-

tained the idea of his attending nearby McGill University and he had conversations with the principal, Sir William Dawson, who became a supportive friend. Further discussions of higher education were curtailed, however, because of the potential cost and the pressures of the busy family farm where his younger brothers were not yet able to provide significant help.

Despite his lack of consistent formal education, John Jack received an excellent informal education in horticulture from his father. By age fifteen he was large and strong enough to do much of the heavy farm work with his father but remembered, "Besides the heavier labor there was always a plentiful supply of lighter work. Of such, pruning, grafting, and budding of trees was probably the most important. My father was my first advisor or teacher in this generally little understood part of horticulture." His parents also allowed him about half an acre of land to cultivate as he chose. With careful husbandry on this plot he could raise crops for sale to earn a small independent income.

A turning point for John Jack came in August 1882, when the American Association for the Advancement of Science (AAAS) conference was held at McGill University. He joined the organization and attended many of the sessions, but more importantly he was able to meet scientists whose papers he had read or with whom he had exchanged specimens. Perhaps the most significant friendship he made that week was of the Cheney family, Mrs. Ednah Dow Littlehale Cheney and her daughter Margaret, a chemistry student at the Massachusetts Institute of Technology. Tragically, Margaret died of typhoid fever the very next month after her return to Massachusetts. She is remembered at MIT by the Margaret Cheney Room, a lounge for the exclusive use of women. Mrs. Cheney wrote to Jack that fall to offer him accommodations in her home on Forest Hills Street in Jamaica Plain so he could attend classes and lectures in Boston and Cambridge that winter. He accepted and came to Boston in November. He soon made the acquaintance of Alpheus Hyatt, professor of zoology at Boston University, and Dr. Hermann August Hagen, professor of entomology at Harvard, both of whom welcomed Jack into their laboratories and lectures.

In March 1883, Jack did not return home to the farm but instead continued farther south to River Edge, New Jersey, and the 80-acre farm of Elbert Sillick Carman, the publisher of the *Rural New Yorker*, a newspaper to which Jack's mother was a regular contributor. Carman ran an extensive experimental agricultural operation and it was hoped that Jack would be able to assist and learn techniques to bring home to Canada. No doubt while he was there he met Carman's daughter Cerise, whom he would later marry in 1907. Unfortunately his time in River Edge was cut short by recurrent malaria and he returned home at the end of August. That winter (1883–84) and the following (1884–85) he returned to reside at Mrs. Cheney's and continue his studies in Boston.

At the Arboretum

John Jack next returned to Boston in the spring of 1886. By this time his younger brothers were finally able to do the heavy farm work with their father so Jack was at liberty to pursue a career elsewhere. He recalled years later, "armed with a letter of introduction ... I went to Professor Sargent's home in Brookline and applied to him for work in the new arboretum which would enable me to get further knowledge of trees and at the same time earn a little money to pay incidental expenses." Charles Sprague Sargent, the director of the Arnold Arboretum, offered him manual labor at first. A short time later, Sargent set him to creating a catalog of the plants in the nursery, a task which coincided with the first planting out of material onto the grounds in their Bentham and Hooker botanical sequence. For the next few years Jack acted in the capacity of a curatorial assistant, preparing herbarium specimens, packaging and distributing seeds, preparing planting plans, mapping the collection, and keeping records of flowering and fruiting. He performed all those duties to a greater or lesser degree throughout his career, but in 1891 he also became "Lecturer at the Arnold Arboretum" and began to conduct springtime classes on trees and shrubs for the general public. They proved to be very popular and additional fall classes were instituted as well. They were finally discontinued in 1908 when attendance dropped off; however, classes

continued in the community and were taught by many of the same people who had originally taken classes from Jack years before.

In the first twenty years of his career in Boston, John Jack was a bachelor of presumably thrifty habits, boarding with Mrs. Cheney in Jamaica Plain. As such, he was able to accumulate enough savings to periodically travel in order to botanize and visit botanic gardens and arboreta. Travel in that period was truly an expedition; it took about a week to reach Europe by sea, and once there, ground transportation was by rail or horse-drawn conveyance. Jack's trips were lengthy, lasting six months in the case of his visit to Asia (see textbox on page 6). He made his first trip overseas in 1891, visiting Paris, Berlin, Geneva, northern Italy, Copenhagen, Hamburg, Brussels, and Britain. He spent several weeks at Kew alone and at

Special Notices.

ARNOLD ARBORETUM OF HARVARD UNIVERSITY.

Mr. J. G. JACK will conduct 15 Field Meetings during the months of May and June, and will explain in a popular manner the character and habits and the economic and ornamental qualities of the trees and shrubs which grow in New England. These meetings will be held on SATURDAY MORNINGS and WEDNESDAY AFTERNOONS, beginning on May 9. The fee for the course will be \$5. Circulars and full information can be obtained from Mr. J. G. JACK, Jamaica Plain, Mass. C. S. SARGENT, Director.
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An announcement for a spring session of John Jack's popular tree classes from around 1900.

every stop was able to meet in person the botanists and horticulturists with whom he had corresponded.

He took another leave of absence in 1898 to explore and report on the forests of the Pikes Peak region, his first exposure to the Rocky Mountain flora. Jack went west again in 1900 to



This image of *Abies lasiocarpa* at Lake Louise, Alberta, Canada, was made by Alfred Rehder in August 1904 while on a plant collecting trip with John Jack.

A JOURNEY TO THE FAR EAST

In 1905, John Jack decided to visit Japan, Korea, and China. He hoped that the things he would invariably learn while abroad and the plants he might find would enrich his teaching and the collections of the Arboretum. For some unknown reason, Charles Sargent was opposed to his trip. He refused to pay for any of Jack's expenses and he docked Jack's pay of fifty dollars a month for the duration of his six-month leave of absence. Undeterred, Jack left Boston at the beginning of July and arrived in Yokohama at the end of the month. He spent the next month and a half visiting gardens, parks, and forests in the area and made an expedition further afield to Nikko and Lake Chuzenji. He decided to alter his itinerary and pay a visit to Sapporo where he was hosted by Professor Kingo Miyabe, whom he had known many years earlier when Miyabe was a doctoral candidate at Harvard University.

From Japan, Jack sailed to Korea where he spent several weeks exploring the region around Seoul. Unfortunately the Japanese government, which had ruled the country since the end of the recently concluded Russo-Japanese War, would not allow travel out of the area, thus precluding any chance of botanical collections outside of the capitol. Jack then traveled to Shandong, China, and then on to Beijing. There he spent time botanizing with his old friend Frank N. Meyer, who was collecting economic plants for the U.S. Department of Agriculture. He returned to Japan in October to spend time with his brother, Milton, and to revisit Lake Chuzenji where he had noted numerous rhododendron and azalea species from which he collected seeds.

He finally sailed for home by way of Naples, Italy, in November, arriving in New York on December 20. Jack considered this trip a success, notwithstanding the recently concluded war between Russia and Japan that hampered his movements somewhat. It cost him some \$2,000, so it came as a pleasant surprise when Sargent, in an uncharacteristically apologetic manner, admitted the great value of Jack's collections and allowed him the \$300 in back pay that had been withheld during the trip.

The library has digitized a collection of John Jack's photographs from Japan, which are available at <http://via.harvard.edu>. A short introduction is available on the Library website: <http://arboretum.harvard.edu/library/image-collection/botanical-and-cultural-images-of-eastern-asia/john-george-jack/>



Japanese black pine (*Pinus thunbergii*) grows above the wall and moat surrounding the Imperial Palace in Tokyo, Japan, in this John Jack photo from August 19, 1905.



John Jack photographed this large specimen of Japanese chestnut (*Castanea crenata*, known then as *C. japonica*) along a road between Narai and Fukusawa, Japan, on September 2, 1905.



In addition to making his own photographs in Asia, Jack also purchased colored lantern slides to use in his lectures. Seen here are two lantern slides from Japan showing people under a wisteria-covered arbor (left) and women digging shellfish on a beach (right).

examine the Big Horn Forest Reserve in Wyoming for the U.S. Forest Service. At the request of Forest Service director Gifford Pinchot, he surveyed the forests of Vermont in 1901. He again went west in 1904, this time in the company of Arboretum colleague Alfred Rehder. They “collected assiduously for the Arboretum, both herbarium and living material,” traveling west on the Canadian Pacific Railroad to Vancouver, then on to Washington, Oregon, and down into California in a stagecoach. Probably the most notable collection from this trip was *Picea glauca* var. *albertiana*, the dwarf Alberta spruce. During all these trips, Jack was busy collecting herbarium material, seeds, and plants for the Arboretum. He was keenly encouraged by Charles Sargent to do so, even though during his times away he was required to take leaves of absence without pay.

Teacher

The Massachusetts Institute of Technology instituted a program in landscape architecture in 1899, headed by Charles Sargent’s nephew Guy Lowell. Sargent recommended that Jack be appointed the instructor in landscape horticulture. His curriculum included dendrology, use of trees in the landscape, creation of planting plans, plant pathology, and practical tree care. Women were admitted to the program (MIT allowed female students while Harvard did not) but in spite of that, enrollment was never very great and competition from a similar course at Harvard sounded its death knell in 1908. During the same period Harvard, in the person of President Charles Eliot, decided that the University needed an undergraduate program in forestry, not associated with the Arboretum, and asked John Jack to be one of the lecturers. He later recalled, “As Professor Sargent was abroad at the time I had to decide. He afterwards told me he would have been opposed if he had been consulted.” It was Sargent’s feeling that one forestry program—the



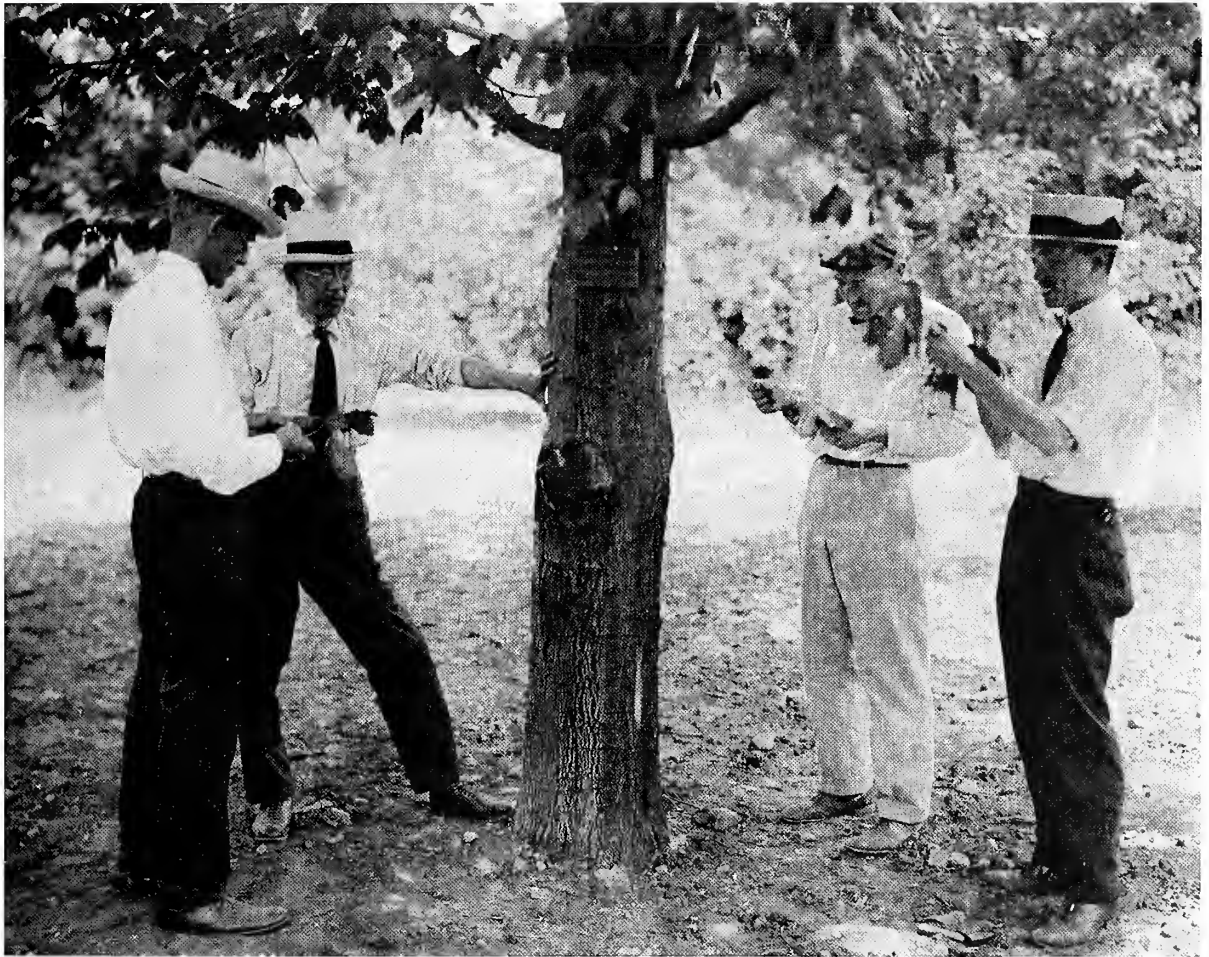
John Jack with a class of forestry students examining trees in the hickory (*Carya*) collection. The photograph is from around 1900.

one at Yale—was plenty for New England. Jack, however, had a different take on it, “I always thought that his real opposition was due to the idea that a forestry department would get money that might otherwise come to the Arboretum, his own pet creation.” The course met on campus during the cold months but moved out to the Harvard Forest in Petersham, Massachusetts, for field studies in the spring and fall. In 1908, Jack was appointed Assistant Professor of Forestry and at about that time the course switched from undergraduate to postgraduate level. Later, Harvard discontinued the forestry school but Harvard Forest continued as a center for research.

The first quarter of the twentieth century saw an influx of Asian students to Harvard. While the Arboretum did not confer degrees, students

could matriculate at the Bussey Institution and then study with John Jack, one-on-one or in small groups. An early student was Woon-Young Chun (Chen Huanyong) who had previously studied forestry at the Massachusetts Agricultural College and the forestry school at Syracuse University and came to study dendrology with Jack in 1915. Students like Chun came halfway around the world to study the tree flora of their native country because of the convenience of having an extensive living collection and a complete herbarium all in one place. In a 1917 interview Chun remarked, "It would take me a lifetime of travel to study what I can find out here about Chinese trees in a few years." One of Jack's most notable Chinese students was H. H. Hu (Hu Xainsu), the botanist who,

along with colleague W. C. Cheng (Zheng Wan-jun), first identified and named living examples of dawn redwood (*Metasequoia glyptostroboides*), a tree previously thought to be extinct but found growing in Hubei in the late 1940s. Hu greatly respected and admired Jack and corresponded with him for the remainder of his life. In a letter dated June 17, 1931, Hu asks Jack for a portrait that they might hang in their herbarium, "Since most of Chinese systematists studied under you and you have exerted such an important influence toward Chinese botany, your photograph is specially needed." In addition to their education at the Arboretum, Jack also brought his students to his property, "Folly Farm," in Walpole, Massachusetts, for practical horticultural training in the garden and orchard.



John Jack (far left) with some of his Chinese students, including Woon-Young Chun to the far right in the boater hat, in a 1917 photograph by A. A. Greenlaw.



× *Sorbaronia jackii*



Rhododendron schlippenbachii



Indigofera kirilowii

JACK'S ACCESSIONS

John George Jack left an indelible mark on the Arnold Arboretum, particularly through the prudent care and attention he gave to the early curation of the rapidly expanding collection. He was also quite the collector of plants himself and over 1,700 accessions originally collected by Jack have moved through the Arboretum. These represent collecting efforts in Asia as well as considerable sampling throughout North America. The majority of his collections did not survive beyond the 1930s, but some 100 accessioned plants collected by Jack do continue to grow at the Arboretum. These include three interesting hybrids, all named in honor of Jack, and some Korean accessions from Jack's 1905 trip to Asia.

Hybrids:

- × *Sorbaronia jackii* – A naturally occurring hybrid between *Aronia* × *prunifolia* and *Sorbus americana* that was collected in 1924 from Halifax, Nova Scotia.
- × *Amelasorbus jackii* – Another naturally occurring hybrid, this time between *Amelanchier alnifolia* and *Sorbus scopulina* that was found in 1918 at Elk Butte, in Clearwater County, Idaho.
- Quercus* × *jackiana* – A naturally occurring hybrid between *Quercus alba* and *Quercus bicolor* whose type specimen was collected by Jack locally in Boston and named by Austrian botanist Camillo Schneider.

Three plants collected in 1905 in Korea:

- Rhododendron schlippenbachii* – One of the most amazing azaleas for both early-flowering displays of large pink blossoms and wonderful gold, orange, and red autumn foliage.
- Hemiptelea davidii* – A monotypic small tree in Ulmaceae, its leaves resemble its relatives elm and zelkova but it also bears formidable spines on its branches.
- Indigofera kirilowii* – A small suckering shrub in the pea family, often used as a ground-cover and bearing racemes of lilac-pink flowers in midsummer.

Legacy

In 1926, Charles Sargent personally asked Jack to go to the Atkins Institution in Cuba, near Cienfuegos in the western part of the island, to collect specimens for the Arboretum herbarium, which lacked material from that part of the Caribbean. He made several trips over the next ten years, sometimes accompanied by special students from the Arboretum. The Atkins Institution was started as a private experiment station at about the turn of the twentieth century to develop better varieties of sugar cane. It was given to Harvard some years later and comprised over two hundred acres of open and forested land populated with Cuban and West Indian woody plants.

In addition to his collections for the Arboretum, Jack also began a herbarium for the use of the Institution containing specimens from their collection as well as other Cuban flora. Karl Sax, Bussey Institution colleague and future director of the Arnold Arboretum, spent time with Jack at the Atkins Institution in 1936. He remembered, "I discovered that although he was 75 years old Professor Jack was up at 6 A.M., worked all day, often travelling into the surrounding country on horseback, and continued to work until 11 or 12 o'clock at night." The Institution remained part of Harvard until 1961 when its director, Dr. Duncan Clement, left Cuba due to pressures associated with the Cuban Revolution and the University ended its support. Today the garden is managed by the Cuban government.

John Jack continued to busily curate the Arboretum collections, to teach, and to collect plant material up until his retirement in 1935 at age 74, the mandatory retirement age imposed by Harvard University. In his later years he lived on his farm in Walpole where he maintained an extensive apple orchard that yielded large crops every year. His wife Cerise had died just after his retirement but his adopted daughter Betty, her husband, and their two daughters shared the farm with him. While pruning in his orchard in 1948, Jack fell from a ladder and broke his hip, leaving him bedridden. He died several months later in 1949, aged 88.

A person like John George Jack would be a rarity today. He was a smart self-starter who made the most of opportunities when they pre-



John Jack in Cuba, April 1927.

sented themselves, and was fortunate to live at a time when it was not absolutely necessary for an academic to have an advanced degree. He was a teacher with an amazing gift for engaging his students, no matter what their background and education might have been. He was a methodical and diligent naturalist, in the broadest meaning of the term, whose interests ranged from entomology to forestry, horticulture, dendrology, and all points in between. The Arnold Arboretum was extremely fortunate that Jack chose to spend his long career here in Boston.

Acknowledgement

We would like to extend our sincerest thanks to Constance W. Cross for her generous gift of John Jack archival materials.

Lisa Pearson is Head of Library and Archives at the Arnold Arboretum.

BOOK EXCERPT

Hemlock: A Forest Giant on the Edge

David R. Foster, Editor

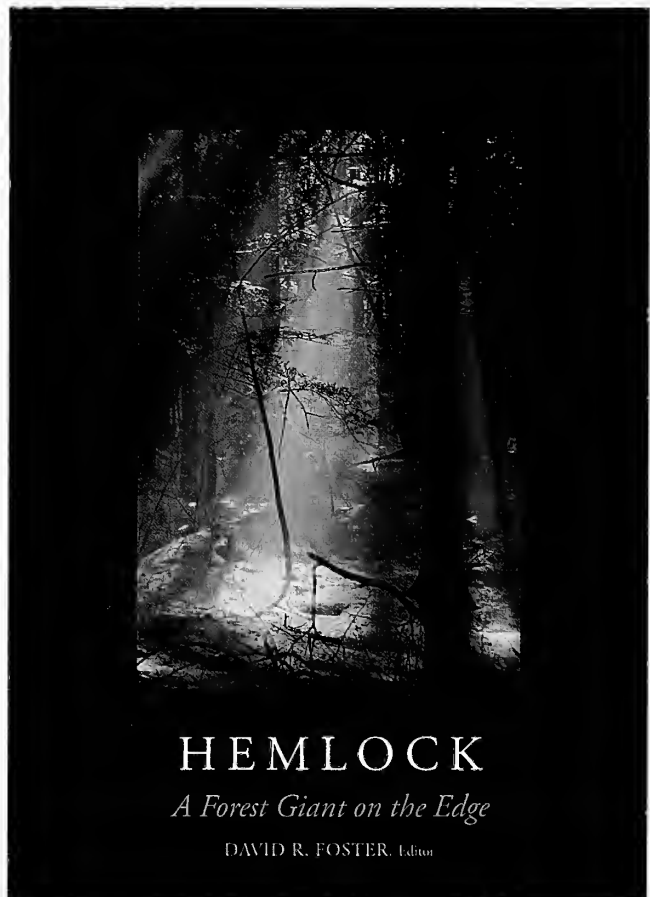
Editor's Note: Eastern hemlock (*Tsuga canadensis*) is an iconic tree species in northeastern forests and the Appalachian Mountains. It has faced peril in the past but is now faced with perhaps its most deadly threat—the invasive and devastating insect pest, hemlock woolly adelgid. In this new book, Harvard Forest director David Foster and several colleagues and scientific collaborators explore the history and ecology of and challenges to the majestic eastern hemlock.

Presented here by permission of the publisher is an excerpt from Chapter Three: *Prehistory to Present*, written by Wyatt Oswald, David Foster, and Jonathan Thompson. In the previous part of the chapter the authors describe the process of extracting 3-inch-wide, 3-foot-long sediment cores from a pond for later paleoecological analyses of the material.

*Hemlock: A Forest Giant
on the Edge*

David R. Foster, Editor.

Written by Anthony
D'Amato, Benjamin Baiser,
Aaron M. Ellison, David
Foster, David Orwig,
Wyatt Oswald, Audrey
Barker Plotkin, and
Jonathan Thompson;
Stephen Long,
Consulting Editor.
Yale University Press.
2014. 336 pages.
ISBN: 978-0-300-17938-5



HEMLOCK has changed in abundance numerous times in the past, and it now faces an extreme threat from the hemlock woolly adelgid. As we seek to consider this new dynamic in perspective, we are fortunate that hemlock has left a remarkable array of records that shed light on its ecology under a wide range of conditions. These historical and paleoecological archives inform the field studies, experiments, and modeling activity that we undertake in the woods and back in the laboratory. A look at hemlock's fossil record helps us examine how hemlock has changed with the intense human activity in the past few centuries and allows us to assess how it might cope with the combination of insect onslaught, climate change, and ongoing human activity today and in the future. It also enables us to evaluate whether there is any hope that hemlock may stave off or recover from the population collapse associated with a new invasive organism.

We use a variety of tools and techniques to reconstruct the historical dynamics of the forest environment and vegetation, as well as individual tree species. To reach back furthest, we study pollen, other microscopic fossils, and diverse signatures of past environments that are preserved for millennia in the sediments of lakes, bogs, swamps, and other wetlands. More recent centuries and decades come alive in historical land-survey documents, field studies of old-growth forests, and tree rings that yield insights into the composition and structure of forest vegetation from the time of European arrival forward. In some cases, the particular qualities of hemlock provide a record that bridges prehistory and history. For example, by carefully dissecting the deep beds of needles that accumulate on the cool, moist ground beneath hemlock, we find pollen and other plant parts that yield a chronological record connecting the postglacial period with the time since European settlement. From these distinctive soil layers comes a record of changes in the composition of individual forest stands that can be linked to the evidence from tree rings, uprooted trees, and the many other clues that are present in the hemlock forest itself. Those of us conducting retrospective studies at the Harvard Forest have employed this full array of approaches, exploiting every opportunity to reconstruct the distribution, abundance, and dynamics of hemlock across New England and going back thousands of years into the past.

ONE HUNDRED and fifty years ago, Henry Thoreau mused in his journal on what stories might be gleaned from the pollen grains accumulating in small pools and ponds, but it took nearly a half century more for the Swedish naturalist and geologist Lennart von Post to first take advantage of this phenomenon in studying the history of plants over long periods. He published a report in 1917 showing that the grains of pollen identified in Scandinavian peats told an astonishing story of dynamic changes in vegetation composition.

Two characteristics of pollen make it a particularly useful tool for interpreting the past. First, pollen grains are remarkably durable because they are shielded by an outer layer of complex chemical compounds that protect the sperms cells as they get transferred from the stamens to the pistils of flowering plants, or from male to female cones in conifers like pine or hemlock. Second, the pollen of different species and genera of plants is different enough to allow us to identify them. It comes in a wide range of shapes, sizes, and surface markings, all of which allow palynologists—the meticulous and patient scientists

who toil over microscopes, examining these minute fossils—to separate and identify the pollen or spores of particular plants. Some pollen can only be distinguished at the level of the plant family (such as roses, buttercups, or peas) or at the genus level (as is the case for oak, which has many different species but unfortunately only a single type of pollen). In other cases, finer distinctions can be made, such as with the pines, the maples, the hickories, and the spruces, where many but not all of the species can be separated. But in the case of two of our most important species—hemlock and beech—we are fortunate that they can be identified individually. Indeed, the pollen of each of these species is rather distinctive. Hemlock pollen grains look like rough spheres with a fringe along their equators. By contrast, each beech grain has three deep furrows with circular pores in the middle. Palynologists puzzle over these and many other distinctions through their microscopes, with the assistance of reference materials, photographic keys, and colleagues. Over time—many years to a lifetime—the many different types of pollen have become readily distinguishable.

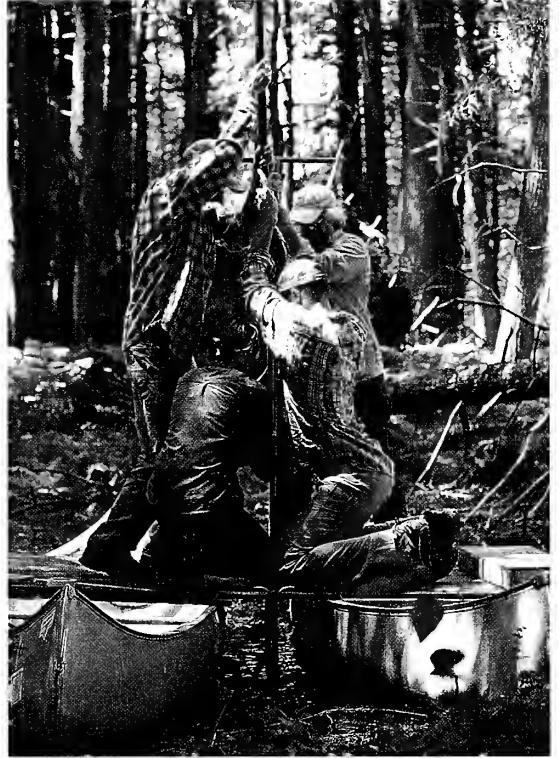
The different pollination strategies of individual species influence how reliably we'll find a particular tree's pollen in the cores we extract. Some species produce small amounts of pollen in an attractive flower to enlist the assistance of insects, birds, and even small mammals to transfer the tiny grains from the flower of one plant to that of another of the same species. The efficiency of this process and the characteristics of these pollen grains, which are often comparatively large, heavy, and sticky, ensure that very few errant grains end up in some sediment. That means that for many plants that use bright and showy flowers to attract the attention of pollinators, there is but a scant record in the mud. Among New England trees, the pollen of chestnut and maple, for example, is largely distributed by insects, so even though these species were or are often abundant, they are underrepresented in the pollen record. If, however, a plant relies on the wind to distribute its pollen grains—and most of our abundant trees such as oaks, birches, beech, and all of our evergreen species use this strategy—it's a different story. These species produce prolific amounts of pollen, each year sending clouds of pollen aloft so that some lucky few might happen upon a female flower.

The vast majority of these pollen grains miss their mark and end up in the sediments of lakes, wetlands, and forest soils. A large lake collects pollen not only from the adjacent vegetation, but also from plants in the landscape as far as ten to a hundred miles away. In contrast, pollen accumulating in vernal pools, small ponds, bogs, or soils is much more likely to be derived from nearby plants, including those hanging immediately above it. This means that records from those types of small basins reflect the local vegetation. Paleoecologists need to take these factors into account in their interpretation of records. They can also apply this knowledge to choose sites that sample the vegetation at either local or regional scales.

Regardless of the site, changes in the pollen grains found in successive layers of sediment indicate whether the composition of the vegetation has changed through time. The key to obtaining a good and continuous record is locating an environment with slow decomposition, in which such layers can accumulate gradually and remain undisturbed. We find such conditions in lakes, where fine-grained mineral and organic matter settle out as mud in the deepest areas and then are preserved in the cold and oxygen-poor environment. An alternative environment is wetlands, where waterlogged conditions inhibit decomposition, and the vegetation grows on a surface composed of the remains of



The top of an eastern hemlock (*Tsuga canadensis*) pokes above the canopy on the Prospect Hill tract of Harvard Forest.



ALL IMAGES BY DAVID FOSTER

Researchers extract sediment cores from Harvard Forest's Hemlock Hollow.



An extracted sediment core is finished and labeled by researchers.



A view of Hemlock Hollow.



In Harvard Forest's Pisgah Tract in southwestern New Hampshire, old-growth eastern hemlocks and eastern white pines (*Pinus strobus*) that were blown down by the 1938 hurricane provide structure to the modern forest.

previous generations of plants. In New England, where glaciers scoured the earth surface during the last ice age, the duration of both of these sedimentary archives is limited to the period since the ice melted, the land surface stabilized, and the climate allowed the growth of plants. Thus, the oldest lake records span about twelve to fifteen thousand years, and many wetlands only extend back five or six thousand years.

MEANWHILE, back in the lab, we slice the cores into thin sections, half an inch or less in length, and carry out a series of treatments and analyses of the material. It's not just pollen grains that we seek. For instance, we want to know the age of the mud at different depths in the core, so we extract small samples of sediment or plant material and send them to a specialized (and expensive) laboratory that assesses the radiocarbon content of the material. We also measure the sediment's organic and mineral content or particle sizes to determine changes in the lake environment, including past droughts, which are often registered as layers of sandy, inorganic material. In combination with other chemical analyses, these sedimentary characteristics provide a detailed record of past variations in climate.

We isolate pollen grains as well as the spores from ferns and other early plants by subjecting mud samples to intense acid baths, washings, centrifuge spins, and sieving steps. It's remarkable that these intense treatments remove most of the organic and mineral material but leave a tiny residual fraction that contains the concentrated and quite intact pollen, along with bits of insects, charcoal, and other miscellaneous detritus. The tiny pieces of charcoal and insect remains, both of which are as highly resistant to decay as pollen, are sieved, identified, and counted under a microscope to provide information about past wildfire activity and insect outbreaks.

We mount the residue on microscope slides and examine them with high-powered magnification, carefully scrutinizing and identifying every pollen grain that is encountered. At any given level, a palynologist might identify 300 to 500 pollen grains through a painstaking process that can take anywhere from two to eight hours or more.

Pollen data tell us the relative abundance of different species. If 50 out of 500 pollen grains at a given level are identified as hemlock, this would yield a value of 10 percent. Knowing whether or not a species is a prolific pollen producer helps us to assess how well the relative abundance of its pollen corresponds to its actual abundance on the landscape. The pollen of insect-pollinated trees such as maple and chestnut rarely exceeds 5 percent of the total, whereas pine, birch, and oak can easily reach 10 to 20 percent or more. Considering these factors, we would assume that 5 percent chestnut means a significant presence. At its very crudest, a pollen diagram will show at what point in the past hemlock or any other plant was absent, rare, or abundant. In most cases, it will also reveal fascinating curves depicting the long-term variation in these species in relationship to other species and many environmental factors.

In well-studied regions such as eastern North America, many dozens of pollen records have been analyzed over the last few decades. In southern and central New England, the Harvard Forest group has analyzed cores from more than three dozen sites. We make the data available to everyone electronically on our website and collaborate with many people who use them. We also keep the cores from which samples have been taken in cold storage for our future needs and those of other scientists who may be interested in examining our records in more detail or for searching for other materials and clues in the mud. Our

network of study sites enables us to understand how the environment and ecosystems have changed in certain places, and how geographic patterns of climate and vegetation have shifted through time. They also help us reconstruct the migration history of various trees, including hemlock, as they returned following the last glacier.

AT THE HEIGHT of the last glacial period, approximately 20,000 years ago, a mile-thick ice sheet covered the New England landscape, with its southern limit extending just to or slightly beyond the modern-day coastline. Pushing and carrying material southward like a combination of a bulldozer and conveyor belt, the immense glacier piled up linear landforms called moraines that today form the higher parts of Cape Cod, Martha's Vineyard, Nantucket, other coastal islands, and Long Island. We use the term "sea level" as if it were a constant, but with vast quantities of water stored on land in these continental ice sheets, the sea level then had dropped more than 300 feet. New England and other coastal regions extended thirty-five miles or more outward on the exposed continental shelf. Pollen records show that, during this peak of ice and cold global temperatures, hemlock thrived far south—in the valleys and hilly landscapes in the Southern Appalachians, where oaks, hickories, and tulip poplars thrive today. As the climate warmed and the ice melted back to the north, hemlock migrated northward, arriving in New England around 10,000 years ago. To get to the Northeast from the Southeast, populations of hemlock had to travel nearly 900 miles in approximately 5,000 years, a migration rate more rapid than we might expect based on our modern studies of the dispersal distances of the species in our forests today.

Most estimates of migration are based on standard observations of the dispersal of a parent tree's seeds and the establishment of new seedlings, which are then extrapolated over time. The small, winged seeds that drop from hemlock cones generally fall within 100 feet of the parent tree, and as a result hemlock moves more slowly across the landscape than most species. For example, in many New England forests today, hemlock has yet to travel the short distances required to return to stands from which it was extirpated two or three centuries ago. In contrast, the seeds of birches and pines may be dispersed 200 feet within a stand and more than 700 feet across an open landscape, enabling them to be highly successful at colonizing abandoned agricultural fields.

Given these factors, we would expect hemlock to be among the slowest of species to have migrated north after the ice age. Indeed, the characteristic slow movement of hemlock initially led to predictions that, during its northward march, it would have lagged well behind the availability of suitable environmental conditions that developed as the climate warmed. Rather surprisingly, however, all current evidence suggests that hemlock and the other major tree species migrated fairly rapidly, effectively keeping up with the climatic conditions that were able to support them. Consequently, the order in which the species arrived in New England fits nicely with our general understanding of their individual environmental requirements, as well as their modern distribution. Open, treeless tundra occupied the harshest climates in the early postglacial landscape. As the climate became more hospitable, the tundra was invaded by northern boreal species—spruce, larch, and birches. With further warming, white pine followed, and then came the truly temperate tree species, including hemlock. Far to the north, the tundra continued to follow the receding glacier toward the pole, and, where they could, boreal forest trees then seeded into the tundra.

Paleoecologists have struggled to reconcile the observed and expected rates of migration and have even given a name to this incongruity: Reid's paradox. The issue has emerged as

one of great importance today because of the looming likelihood of rapid climate change and the question of how plants will respond and cope with new conditions. We are employing all sorts of approaches—genetics, simulation modeling, field and laboratory studies of dispersal, and pollen analysis—as we continue to grapple with the question. Have we overestimated the rates at which trees moved in the past, or are we underestimating their anticipated and potential future dispersal rates? One possible way to account for a more rapid past dispersal is to invoke a history of rare long-distance dispersal events, such as abrupt gusts and updrafts in wind that may loft a seed into the jet stream, or the rare flight of a bird in which it carries a seed for dozens of miles. In this way, a chance event can disperse seeds great distances. If such an event happened even once a decade, it may have been extremely important in shaping patterns of movement over centuries. We cite uncommon processes such as these in our modeling discussions when talking about the dispersal of insects like the hemlock woolly adelgid or the adaptations of plant species under future climates. As research on this dilemma progresses, the answers to these questions will have important implications for predicting the future shape of our forest ecosystems and for gauging the ability of many species to survive the expected changes in climate in coming decades.

The long-term history of hemlock also reveals the extreme malleability of forest types and assemblages, including those that are familiar to us today. Hemlock arrived in the northeastern United States about 2,000 years after white pine and 2,000 years before American beech, even though today it frequently grows alongside both these species, and we often think of them as members of the same plant communities. Given beech's similarity to hemlock in shade tolerance and suitability for forest canopies, and the manner with which they coexist in many places today, it is hard to imagine that hemlock grew in New England for 2,000 years without beech. Similarly, it was only with the arrival of hemlock that the New England landscape developed forests akin to the old-growth stands of white pine and hemlock studied by early ecologists and described in many Harvard Forest studies, including those by Richard Fisher, Bob Marshall, Tony D'Amato, and Dave Orwig. The contrasting histories of these various trees illustrate that species respond in highly individualistic ways to environmental change. Because conditions in the past were distinctly different from the present, we witness the species behaving in significantly different ways over time. The assemblages of plants and animals that are familiar to us today are actually quite ephemeral in deep time and space.

It is through such understandings that we've developed an ecological theory that accepts and explains the separate though interactive behavior of species. One of the earliest and best articulations of this theory came from a noted northeastern botanist—Henry Gleason of the New York Botanical Garden—who developed the “individualistic concept of ecology” in the early 1900s. This simple but revolutionary theory posited that the makeup of vegetation on a site was determined by the actions of the many individual species, each of which operated quite separately from others and according to its unique ecological qualities. Although this concept was debated for decades, some of the strongest evidence that led to its conclusive support came from paleoecological studies that showed the highly disparate behaviors of different tree species in migration and in response to climate change and to natural and human disturbances. While this understanding of plant behavior and ecology emerged from the past and helps us explain our current landscapes, it should also prepare us for unanticipated combinations of species to appear under the anomalous conditions expected for the future.



Dead trunks of American chestnut (*Castanea dentata*) intertwined with dying eastern hemlocks.

Coring dozens of ponds and bogs and examining tens of thousands of pollen grains preserved in their sediments has helped us outline the following picture of New England's prehistory. After a lengthy dry period, from around 11,500 to 10,000 years ago, during which white pine dominated the landscapes of the northeastern United States, hemlock increased in abundance across much of New England, then reached its peak population levels during a relatively warm and moist interval from 8,000 to 5,500 years ago. Beech had arrived to join hemlock in the region at that point, and with oaks, birches, and maples also present, and white pine and pitch pine already well established, the overall composition of New England forests was quite similar to what we find in our landscape today. Although the environmental conditions of that earlier time appear to have been well suited for hemlock, some of our recent research suggests that brief periods of cold climate occurred every few centuries, with deleterious impacts on hemlock in some parts of New England. Various lines of evidence, including chemical analyses of lake sediment records, show that the generally warm, moist conditions were interrupted occasionally by a century or so of cold, dry climate. And while hemlock and other species did not always respond uniformly to these events across the region, some of our relatively detailed pollen records feature abrupt, short-lived declines of hemlock, including significant population reductions at around 8,000 and 6,000 years ago. Hemlock certainly didn't disappear from the landscape during these events, but the pollen data do suggest that it became much less abundant during times of cold, dry conditions.

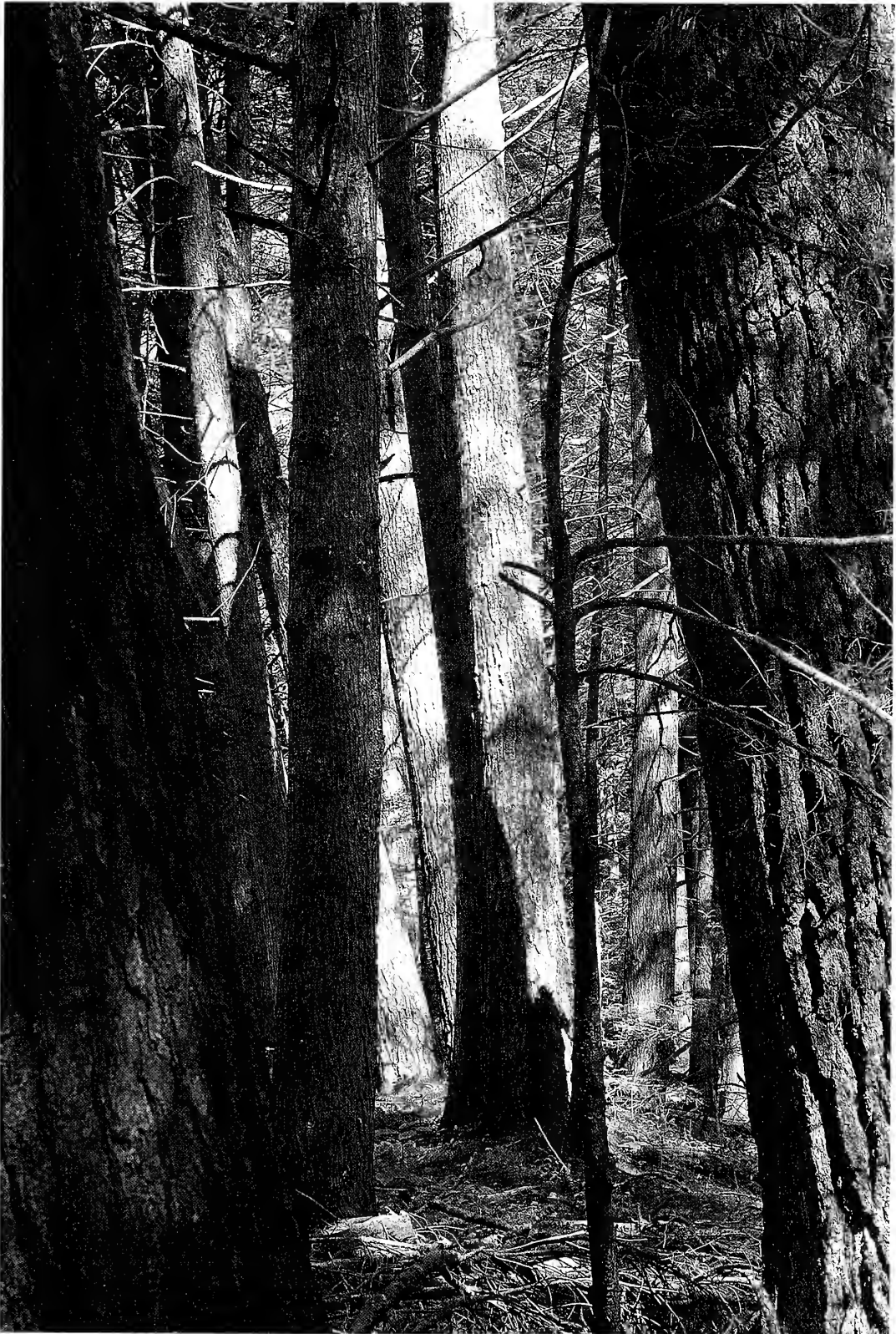
Then, around 5,500 years ago, hemlock experienced an abrupt, range-wide collapse. For about two millennia it nearly disappeared throughout its entire range in the Northeast before it rebounded about 3,500 years ago. Although it recovered greatly across the region, at most sites hemlock never returned to its predecline levels. This hemlock decline is one of the most thoroughly studied aspects of the postglacial vegetation history of North America, yet we still don't completely understand what caused it or sustained it. Conclusions drawn over the past three decades variously attribute hemlock's decline to a species-specific disease, a massive insect outbreak, a sustained shift to drier climate, a series of drought events, and a combination of these factors. It is now quite clear that climate was strongly involved and that in some ways the big decline was a larger version of the earlier declines witnessed during cold spells. If the trees weren't killed directly by drought, then the associated environmental conditions either stressed hemlock in ways that made it more susceptible to insects or disease or facilitated an unusual outbreak of a pest or pathogen. (It was this record of minor events leading to the major drought and decline in hemlock that our colleague correctly surmised he was seeing in the various layers of sand we observed that day on the raft in the middle of the lake.)

Hemlock eventually recovered, and pollen records reveal that it was again abundant in New England forests from around 3,500 years ago to the time of European settlement. Our studies of the sediments of Hemlock Hollow, a vernal pool hidden in the large hemlock forest on the Prospect Hill tract of the Harvard Forest, have yielded a detailed stand-scale record of forest changes over the last 10,000 years. The local nature of this record enables us to examine the fine-scaled ecological response of an individual forest to various changes in its environment. Here we can see that when disturbances occurred, including fires every 1,000 to 3,000 years, hemlock abundance dropped abruptly and then rebounded slowly, taking 500 years or more to recover to original levels. In the recovery from these major disturbances—intense events that we interpret to have killed most of the larger trees—the

successional sequences brought back the species that we know so well and comply exactly with our understanding of the modern ecology of New England forests. For much of the pre-European period when hemlock declined, it was replaced around Hemlock Hollow by some combination of early successional and rapidly reproducing and growing species—white pine, birches, and other hardwoods—as well as more mid-successional, long-lived species such as oaks.

Everything changed when chestnut arrived. After spending the ice age in the southeastern United States, chestnut slowly migrated north and finally arrived in New England 2,000 years ago. At Hemlock Hollow we see chestnut employing its phenomenal ability to sprout and its rapid growth rate to become the dominant species when the populations of hemlock and other species were reduced by disturbance. This pattern occurred following fire and also after European settlement and the first episodes of logging in these forests. These disturbances affected both species, but chestnut bounced back quickly. Dead chestnut boles are a common sight in many hemlock forests today; it is clear from the fossil record at places such as Hemlock Hollow that the two species had a close and often reciprocal relationship in the more distant past. One other notable observation emerges from the long-term record at Hemlock Hollow: regardless of the nature of the disturbance or the successional species that followed it, in each case, hemlock recovered from the disturbance and eventually returned to dominance. These records offer other instructive insights into the broader nature of the New England landscape and its forests. The low abundance of charcoal in lake sediments confirms that there was little fire. Meanwhile, the long duration of hemlock dominance confirms that the region was only infrequently affected by fire or any other major disturbances: drought, wind, and ice. Similarly, there is no direct evidence of disturbance to or use of these forests by the dispersed populations of largely hunting and gathering American Indians who inhabited central New England. Thus, while we may assume quite correctly that change is a prominent factor in forest ecosystems, the paleoecological perspective demonstrates that New England hemlock forests experienced lengthy periods of relative stability.

We also have a detailed map of North American forests just before they were first cut and then cleared. For this we can thank a largely anonymous group of seventeenth- and eighteenth-century land surveyors. While walking the landscape and demarcating it into towns, sections, and ownerships, colonial surveyors recorded the presence of individual trees by their species and sometimes by their size. Ecologists have been using these accidental forest inventories to reconstruct presettlement forest composition for almost a century. By far the most common source for survey records has been the Public Lands Survey of the General Land Office, which was established by Thomas Jefferson and covered much of the midwestern and western states. But because southern New England was largely settled prior to the establishment of the General Land Office in 1785, its survey records are much less standardized. Survey-based reconstructions of New England forests typically rely on some type of town proprietor records. The English colonies deeded unsettled land in the form of regularly shaped towns, often about six miles square. In laying out the boundaries in these towns, surveyors identified and blazed “witness trees” as permanent markers at the corners of individual lots ranging in size from 1 to 160 acres. Longtime Harvard Forest collaborator Charlie Cogbill has spent decades amassing a comprehensive spatial database of these tree records from across the Northeast. The maps derived from his witness-tree data set have been analyzed by Jonathan Thompson to show how forest composition varied across the region.



Eastern hemlocks and eastern white pines along the Swift River in Petersham, Massachusetts.



Old eastern hemlocks and eastern white pines in Harvard Forest's Prospect Hill Tract.

In northern Maine, spruce, balsam fir, and white cedar dominated the landscape. Moving slightly southward into the rest of Maine, New Hampshire, and Vermont, hemlock, beech, maples, and red spruce were common, even reaching down along the broad uplands of the Berkshires in western Massachusetts and Connecticut. Oaks, pines, hickories, and American chestnut picked up from there and were prevalent in the south and along the coast. In broad detail, this pattern closely parallels the regional environmental gradient, with cooler and moister conditions to the north and warmer and drier conditions to the south. Hemlock became less common farther south and was found in increasingly smaller concentrations. Near the coast it would only have occurred in isolated stands in protected moist areas.

Pollen records provide context for the witness-tree snapshot of New England vegetation patterns, including some perspective on the dynamics that were under way when the European settlers arrived. For example, we can see that American chestnut was the last tree species to reach New England from its glacial refuge in the Southeast, arriving here only in the last 1,000 to 2,000 years. Meanwhile, hemlock and beech appear to have already begun a slow decline a couple of centuries before colonial deforestation commenced. The timing of these declines seems to coincide with the Little Ice Age, a relatively recent climatic interval (A.D. 1550–1850) that triggered physical and ecological changes in many

regions of the world, including glacial advances farther north. It may seem counterintuitive that two species common in northern New England would be bothered by a shift to colder climate. It is quite possible, however, that conditions became both colder and drier, with both hemlock and beech suffering due to their relatively high moisture requirements.

The latter part of the Little Ice Age coincided with the expansion of European colonists across New England, transforming the land. Region-wide, up to 60 percent of the land was cleared for agriculture and the rest was cut—repeatedly in some places—with a peak in harvesting occurring in the late nineteenth and early twentieth century. Although forest once again covers more than 80 percent of New England, these second-growth stands are not the same as those of presettlement times. When we compare the witness-tree data with present-day forest composition, we find that some species are more common than they were centuries ago, such as early successional birches, red maple, and pines, including the old-field white pines that invaded abandoned agricultural lands. These light-seeded, fast-growing, and light-requiring species spread and grew rapidly across heavily disturbed areas, thriving after the intense farming and logging subsided. On the other hand, some species are less abundant than they were before European settlement. Species of mature forests, including hemlock and beech, are much less common than they were in the witness-tree surveys. Throughout the Northeast, hemlock declined as much as 10 percent over the last 400 years.

When we zoom back in from the region-wide scale to that of the individual landscape, we often see considerable evidence of land use in the characteristics of hemlock forests. In some cases, seemingly ancient hemlock stands have undergone much greater changes in their recent past than we might at first assume. These are the unexpected findings of a study led by Harvard Forest researchers Jason McLachlan and David Foster. They set out to reconstruct the histories of four old hemlock forests in central Massachusetts, using both tree-ring analysis of the largest trees and centimeter-by-centimeter analyses of pollen grains preserved in the approximately six-inch-thick layer of organic matter forming the top layer of the soil. They found that the stands, dominated today by hemlocks 100 to 200 years old, had experienced a series of disturbances over the last few centuries, including logging, windstorms, fires, and pathogen outbreaks. Indeed, early and mid-successional trees such as oaks, pines, and American chestnut had occupied those same stands at different times in the past. In many of the forests, it appeared as though today's dominant hemlocks may in fact owe their current good fortune to the removal of competing species by selective logging and the chestnut blight.

Like many of our other retrospective investigations of hemlock, this study of second-growth stands obliges us to change the way we think about the species, the forests it forms, and the way that nature operates. On one hand, forests that appear to be unchanging may be relatively recent in origin and shaped by processes that the species has never experienced before. On the other, although hemlock forests have been dynamic at times, the history of the species in New England has always been one of long-term dominance interrupted by infrequent abrupt declines. With such a decline spreading across the landscape today, we can expect another lengthy period with little hemlock followed by—we can only hope—its gradual return.

Getting Buzzed at the Arnold Arboretum

Callin Switzer

While strolling through the Arnold Arboretum during the summer, visitors may see bees flying from flower to flower. Some bees are pushing their heads deep into flowers and collecting nectar, others are more interested in collecting pollen from the flowers' anthers. Bees that collect pollen are not collecting most of it for themselves; they are taking it back to their colony to feed to the larvae. Pollen provides a protein and mineral source for the developing brood.

In flowering plants, pollination is the process of moving pollen from the anthers to the stigma. As bees collect pollen and nectar, they inadvertently transfer pollen from the anthers of one flower to the stigma of another flower, either on the same plant or different plants. For plants that are self-incompatible (they cannot reproduce without cross pollination from another plant), this transfer service is essen-

tial. For both self-incompatible and self-fertile species, the transfer of pollen between plants allows for genetic variation in the plants' offspring, preventing plant populations from becoming inbred. Without bees, many species would make neither fruit nor seed.

Give It Up for the Bees

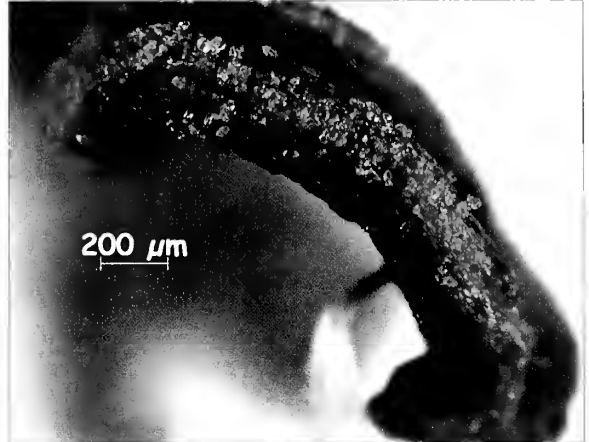
Plants have developed a variety of ways to "give" their pollen to bees. Some have longitudinally dehiscent anthers; these split open down the sides when the pollen is ready, making it easily accessible. Longitudinally dehiscent anthers have benefits and drawbacks. One benefit is that plants with these anthers can be pollinated by many insects, birds, or even humans. (In Sichuan, China, the decline of pollinators has led to pollination of apple and pear orchards by humans armed with vials of pollen and small brushes.) These plants are generalists



Buzz pollination helps produce plump tomatoes like these (*Solanum lycopersicum* 'Lemon Boy').

Pass the Bees, Please

The next time you dip into a bowl of salsa, serve up butternut squash soup, or savor a slice of blueberry pie, thank the bees. Tomatoes, squash, apples, blueberries, and lots of other delicious foods require pollination—mostly done by bees. About 30 percent of our food relies directly on pollinators, and thousands of plant species depend on bees for reproduction. Honey bees and bumblebees are major pollinators of food crops, but many other bee species also pollinate a wide range of plants.



ALL PHOTOS BY THE AUTHOR UNLESS OTHERWISE INDICATED

The anthers of Chinese Stewartia (*Stewartia sinensis*) (left) and Carefree Beauty rose (*Rosa* 'Buchi') (above) are longitudinally dehiscent, which means that each anther splits along its length to release pollen.



A bitterweet nightshade (*Solanum dulcamara*) flower, showing poricidal anthers. At the center of the flower, ten distinct pores are visible. Pollen is held in the tubes below the pores.

when it comes to attracting pollinators, but this could also be seen as a drawback. What if an animal rushes by and knocks all the pollen off the flowers? What if an insect visits different species and never actually transfers pollen between conspecifics (members of the same species)? Changing the shape of the anther can help solve both of these potential problems.

Multiple lineages of plants have evolved anthers that are tube-shaped. Instead of splitting down the sides, these anthers simply open tiny pores when pollen is ready to be released. These anthers are known as poricidally dehiscent, or poricidal.

Poricidal anthers help keep pollen from being knocked off the flower, and they prevent many pollinators from reaching the pollen. About eight percent of flowering plants (some 20,000 species) have poricidal anthers (Buchmann 1983). Because the pollen is in a tube, animals cannot easily shake it free. Three common ways to access this pollen are biting through the outside of the anther; squeezing pollen out by treating the anther like a tube of toothpaste; or



Purple beautyberry (*Callicarpa dichotoma*) has poricidal anthers; a pore is visible on the lower edge of the anther on the right in this photo.

vibrating the anther to eject pollen out the hole. Bumblebees (*Bombus* spp.), some of the most common pollinators in the Arnold Arboretum, employ the technique of vibrating pollen out of the anthers. This technique is known as buzz pollination, and every summer many flowers “get buzzed” at the Arboretum.

Good Vibrations

Some of our favorite fruits and vegetables are efficiently fertilized by buzz pollination—these include blueberries, tomatoes, eggplants, and cranberries. Honeybees (*Apis mellifera*), the most common pollinator in the United States, cannot buzz pollinate (the reasons for this are not clear). This means that we must rely on bumblebees and other buzz-pollinating native pollinators to fertilize these crops. For example, greenhouse tomato growers often place colonies of bumblebees in their greenhouses to pollinate the tomatoes.

In flight, bumblebees flap their wings at about 190 cycles per second, or hertz (Hz); this vibration sounds like the F-sharp below middle C on a piano. If an average eye blink lasts for about 300 milliseconds, that means that bees flap their wings over 50 times while we blink. Bumblebees use their flight muscles for another purpose as well: creating the vibrations needed for buzz pollination. After a bumblebee lands on a flower and decides to try buzz pollination, she folds her wings into their resting position over the abdomen. While the wings are decoupled from flight muscles, she contracts the muscles that normally power wing strokes. Bees’ flight muscles are not directly attached to the wings, but instead to parts of the thorax. One group of muscles attaches to the top and bottom of the thorax. As these dorsoventral muscles contract, the thorax deforms. The sides of the thorax are pushed outward as the top and bottom of the thorax are pulled together. Another group of muscles attaches to the front and back of the thorax. These longitudinal muscles contract and the dorsoventral muscles relax. This deforms the thorax differently—now the top and bottom of the thorax get pushed outwards as the front and back of the thorax get pulled together. This whole cycle happens with every wing stroke when the wings are engaged,

but while the wings are decoupled, the thorax experiences this cyclic deformation while the wings stay relatively stationary. The thorax usually deforms at a higher frequency during buzz pollination than during flight. Although the bee is not moving a large distance with each deformation of the thorax, the accelerations are huge! One species of bumblebee has been found to buzz with accelerations nearly 20 times the acceleration due to gravity (De Luca and Vallejo-Marín 2013). This produces forces high enough to expel pollen out of the anthers, where the bee can then gather it easily.

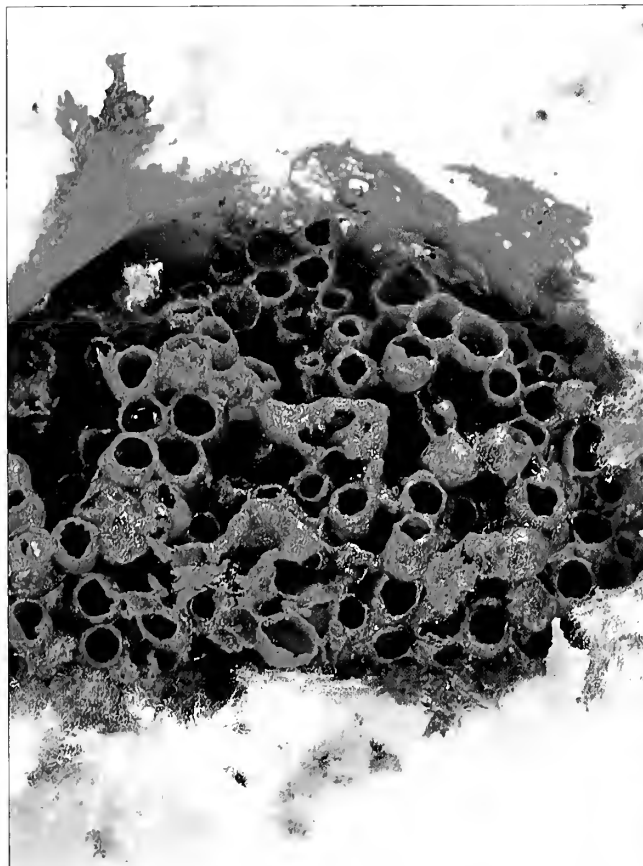
Characterization of Buzz Pollination at the Arboretum

During the summer of 2013, I spent over a month at the Arnold Arboretum, characterizing the buzzing behavior of bumblebees. I usually arrived early in the morning and made a bee-line for the Leventritt Shrub and Vine Garden, where I could easily access flowers that were abuzz with pollinators.

I used a microphone to record the sounds the bumblebees made while flying, buzz pollinating, and just buzzing in irritation. Bumblebees’ typical behaviors made data collection easy. For one, bumblebees were unfazed by my presence—I could hold a microphone just a few centimeters from their bodies while they were collecting pollen and they still were not scared away. Another behavior that made data collection easy was that bumblebees very habitually forage on the same flowers (Heinrich 1976). If I did sear a bee away, I could rely on it to come back soon. To get wingbeat frequency, I followed the bee from flower to flower, recording a few segments of flying and buzzing. Last, I captured the bee in a net, and jostled the net around. This caused the bee to irritation buzz, which I recorded from the outside of the net. I used a computer program to calculate the Fast Fourier Transform (an algorithm) on segments of these recordings to get the wingbeat, buzz pollination, and irritation buzz frequencies. During buzz pollination and irritation buzzing, the bumblebees’ wings stayed folded over the abdomen. After recording over 350 individual bumblebees while they were foraging, I found an average buzz polli-



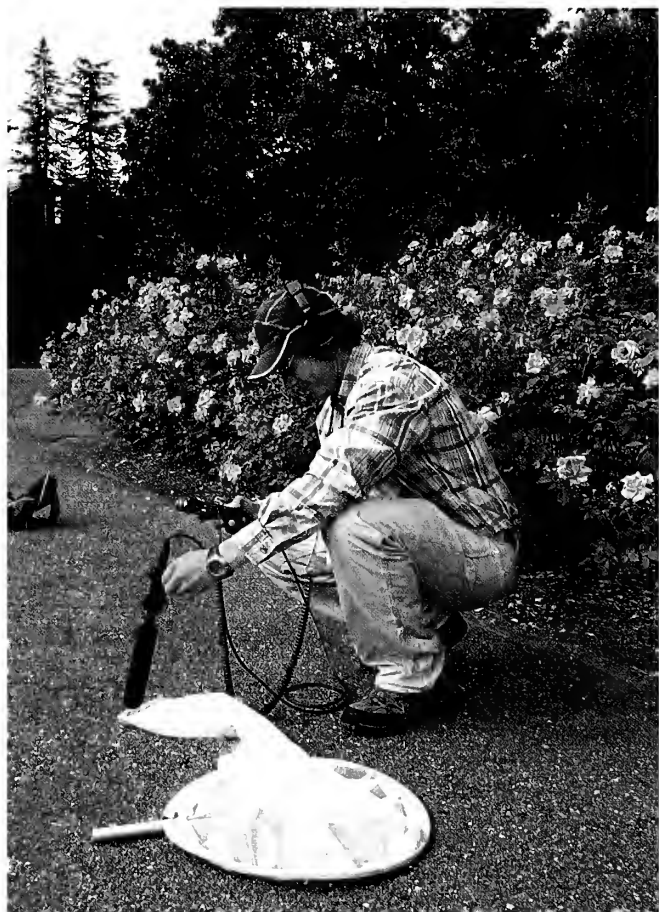
Look closely, and you can identify bumblebees and honeybees. Honeybees (left) are more slender and brown. They usually have rings of grey on their abdomen. Bumblebees (right) are round, fuzzy bees, often with black on the abdomen and yellow on the thorax.



A common eastern bumblebee (*Bombus impatiens*) nest that was reared in a lab; the cotton covering has been pulled back to expose the cells. Nests are typically built in preexisting holes, often below ground. The structure is mostly made of wax, which is secreted from between the segments of a bumblebee's abdomen. A typical bumblebee colony has 50 to 200 individuals at a time. Food is stored in some of the cells, while other cells contain brood in various stages of development.



Common eastern bumblebee (*Bombus impatiens*) buzz pollinating a Chinese beautyberry (*Callicarpa cathayana*) flower.



The author collecting audio recordings of bumblebees foraging on Carefree Beauty roses (*Rosa* 'Bucbi') growing near Rehder Pond at the Arboretum (left) and the irritation buzzing of briefly netted bumblebees (right).

nation frequency of about 270 Hz. The pitch of this vibration frequency is equivalent to a C-sharp above middle C on the piano. Through this research I was able to answer some basic questions about buzz pollination, but my observations also led to more questions.

Answers about buzz pollination:

- Q. Can bumblebees change the frequency at which they buzz?
- A. Yes. Without extending their wings, individual bumblebees can increase their buzzing frequency by at least 90 Hz.
- Q. Do bumblebees buzz pollinate at different frequencies on different plants?
- A. Probably. My data show different buzz pollination frequencies on different plants,

but it's possible that the differences arose because the plants flowered at different times of the year and samples were done in uncontrolled humidity. Future experiments in a more controlled setting will compare flowering plants at the same time of year and at the same humidity, which will provide more definitive results.

- Q. What other conditions affect vibration frequency during buzz pollination?
- A. Humidity and time of year. Out of all the conditions (including bumblebee size, temperature, and time of day), these were the two conditions that had the greatest effect. Bumblebees tended to buzz at higher frequencies in high-humidity conditions and at the beginning of the summer.

I recorded bumblebee buzz pollination on the following plants at the Arboretum. There are a number of other plants in the collections that are buzz pollinated, including *Vaccinium* species such as lowbush blueberry (*V. angustifolium*).

<i>Callicarpa cathayana</i>	Chinese beautyberry
<i>Callicarpa dichotoma</i>	Purple beautyberry
<i>Callicarpa japonica</i>	Japanese beautyberry
<i>Diospyros virginiana</i>	Common persimmon
<i>Hypericum</i> 'Hidcote'	'Hidcote' hybrid St. John's wort
<i>Lespedeza bicolor</i> 'Natob Strain'	'Natob Strain' shrub bushclover
<i>Rosa</i> 'Buchi'	Carefree Beauty rose
<i>Rubus odoratus</i>	Fragrant thimbleberry
<i>Stewartia sinensis</i>	Chinese stewartia



The anthers of common persimmon (*Diospyros virginiana*), seen in the center of these flowers, are not technically poricidal but they do dehisce only partially.



Fruit of purple beautyberry in autumn.

New questions about buzz pollination:

1. Are all bumblebee species equally good at buzzing?

I observed many individuals of the common eastern bumblebee (*Bombus impatiens*) collecting pollen by buzzing. However, I observed a number of two-spotted bumblebees (*Bombus bimaculatus*) collecting pollen without buzzing. This was happening on St. John's wort (*Hypericum* 'Hidcote'), which was being buzz pollinated by other bees. More controlled experiments on dif-

ferent bumblebee species will provide more information on this topic.

2. Why is the Arboretum dominated by a single bumblebee species?

I found at least five bumblebee species pollinating. However, out of nearly 400 bumblebees, I found 375 individuals of the common eastern bumblebee; that is about 95%. It would be interesting to survey bumblebee species at other habitats (i.e., city vs. rural) to see if common eastern bumblebees are also dominant in those locations.



A bumblebee on a buttonbush (*Cephalanthus occidentalis*) inflorescence at the Arboretum.

3. Why do buzz frequencies change?

Could it be that different flowers require different frequencies to get maximum pollen release? Is humidity affecting the bumblebee or the flower more?

4. Why do bumblebees buzz on plants with longitudinally dehiscent anthers?

Before I started collecting data, I thought that bumblebees shouldn't buzz on longitudinally dehiscent anthers since the pollen is readily accessible. But I found multiple instances of buzz pollination occurring on St. John's wort (*Hypericum* 'Hidcote') and Care-free Beauty rose (*Rosa* 'Bucbi'), and I even recorded some buzzing on Chinese stewartia (*Stewartia sinensis*). All three of those plants have longitudinally dehiscent anthers. Stephen Buchmann (1985) published similar observations and hypothesized that buzzing may increase effectiveness at collecting pollen on longitudinally dehiscent anthers, especially when the flower has a "shaving brush" structure (contains numerous stamens with long filaments). One suggestion for why bumblebees use buzz pollination on this type of flower is that it allows them to get pollen from many anthers at one time. With these flowers, bees gather many anthers together and hold them close to their bodies while they buzz. Though this doesn't require buzz pollination, buzzing could result in faster pollen collection than collecting from one anther at a time.

Conclusion

Answering questions about bumblebee pollination can help humans effectively manage plant populations, including our food supply. Spending 30 days in the Arboretum helped me answer a few pollination questions, but there are still lots of unanswered questions. The next time you walk through the Arboretum (or your own yard) try to identify some of the most common pollinators. By looking closely at the shape of flower anthers and how they dehisce (open), you can make a guess about what type of bee pollinates the plant. And the next time you're eating



Bumblebees were observed buzz pollinating the flowers of St. John's wort (*Hypericum* 'Hidcote', seen here) even though it does not have poricidal anthers.

blueberries or combing through a recipe book to find something to do with all your tomatoes, you can thank the bees.

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Callin Switzer is a graduate student in Stacey Combes's research lab at Harvard University.

2013 Weather Summary

Sue A. Pfeiffer



A light snow in late February flocked trees along Meadow Road.

JANUARY was a relatively warm and dry month. The first two-thirds of the month saw high temperatures mostly in the high 30s and 40s (°F) with occasional days in the 50s and even 60s. Precipitation was minimal during this period with only one snowfall event, which accounted for half of the monthly total. This beautiful weather created ideal pruning conditions on the grounds, but was followed by an arctic cold front that saw temperatures dip to below freezing for ten days straight. The last two days of the month saw temperatures return to the 60s as a storm system dropped a half inch of rain and brought high winds to the area, including gusts of over 40 mph.

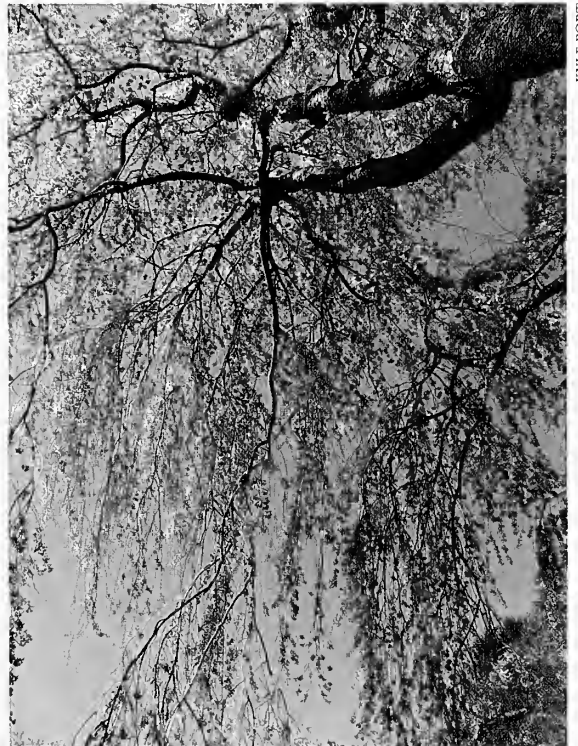
FEBRUARY temperatures were average as high levels of precipitation, more than double the average, fell during the month. Almost 7 inches of rain equivalence was recorded, with a storm event occurring on every weekend. Only a dusting of snow was received the first weekend but a week later, on the 8th and 9th, a nor'easter rolled into the area and dropped 25 inches of snow. High winds (20 mph sustained winds with gusts reaching 38 mph) accompanied the rapidly accumu-

lating snow, which made any sort of transportation a challenge on snow-covered roads and sidewalks. Temperatures warmed during the following week, reaching above 40°F each day (even hitting 50°F on one occasion). The rapidly melting snow created tiny natural streams throughout the landscape. The following weekend brought a mix of snow and mostly rain with high winds returning once again. A large winter storm was predicted to hit Boston on the final weekend of the month, but luckily the snow-rain line remained north of the Arboretum and the grounds received an additional 1.25 inches of rain. Temperatures stayed warm as the next front moved in; the final days of February saw additional heavy rain, which melted away all remaining snow.

MARCH was a seasonable month in terms of both temperature and precipitation. A major storm early in the month dropped 19 inches of wet snow over a two day period (7th and 8th). Warm temperatures following the snow event caused all snow to melt within a four day period, leaving no sign of the storm. The final measurable snowfall of the season was on the 19th; we welcomed spring the following day. The month ended with temperatures hitting 60°F and almost no signs of snow remaining. Warm temperatures, melting snow, and precipitation left the soil plenty moist and puddles were visible in low lying areas.

APRIL temperatures were average but rainfall fell far below average. April started off cool and dry, as puddles receded and moisture levels in the soil diminished. Spring growing degree days began accumulating on April 8th as temperatures warmed. A number of smaller storms, including one quick-moving thunderstorm, dropped minimal precipitation during the second week. Two slower storms over the following couple of weeks delivered much-needed precipitation. We ended the month with a whole week void of rain, which led to high amounts of lingering pollen in the air. The moderately cool, dry weather was favorable for cherry trees and their bloom time was extended, creating a spectacular show along the *Prunus* Promenade in the Bradley Rosaceous Collection.

MAY started off dry as the first week was devoid of any precipitation. Up to this point, we had received only 1.6 inches of rain over the previous seven weeks. Despite this lack of moisture, the landscape remained lush and colorful as trees and shrubs continued to leaf out. The week leading up to Lilac Sunday brought significant amounts of rain, which carried into



KYLE PORT

Cool, dry conditions in late April were perfect for allowing an extended cherry blossom season in the Bradley Rosaceous Collection. Seen here, the graceful branches of *Prunus subhirtella* var. *pendula* 'Park Weeping' (accession 412-62-A).

KYLE PORT



A *plein air* artist paints in the lilac collection on May 10, two days before the 2013 Lilac Sunday celebration.

KYLE PORT



Arboretum arborist Bob Ervin surveys an eastern hemlock (*Tsuga canadensis*, accession 2863-98-A) struck by lightning in a May storm.

the morning of the 12th, Lilac Sunday. But by noon the rain had ceased and the sun was out to welcome all visitors with temperatures in the 70s. Cooler temperatures and dry conditions returned during the following week as warm, sunny weather later moved in. This warm spell was followed by a number of smaller rain systems; we received rain on 10 of the last 12 days of the month, accumulating 3.38 inches of precipitation. The heat arrived as we saw temperatures in the high 80s and low 90s to end the month.

JUNE was an extremely wet month with average temperatures. The month began as May ended, with hot and humid weather. Temperatures were in the high 80s and low 90s before a cold front rolled in, bringing ideal early summer conditions: sunny and warm with highs in the 70s. The beautiful weather did not last long as remnants of tropical storm Andrea arrived on the evening of the 6th and lasted until the morning of the 8th; we received 3.6 inches of precipitation. The next storm rolled through on the 10th and 11th, dropping an additional 1.68 inches of rain. Despite these storm systems, no major damage was recorded; soil was saturated with puddles in low lying areas. A couple of days later, a fourth storm dropped 2.03 inches of rain, which added to the already saturated ground. As if the over 8 inches of rain received during the first two weeks of June weren't enough, the last two weeks of the month saw additional rain events including four separate thunderstorms. By the time we reached the 30th, we had received a total of 11.37 inches of rain, more than three times the monthly average.

JULY was a warm month with average rainfall. High heat and humidity were prevalent during the first week as we experienced a four day heat wave starting on Independence Day. A cold front moved in thereafter providing temporary relief and a small amount of rain before a prolonged heat wave began mid-month. The seven day event brought high humidity and temperatures reaching the mid-90s. The high heat in combination with the humidity created

oppressive and uncomfortable conditions outdoors, the heat index reaching 108°F. The final ten days of the month saw more comfortable conditions return with temperatures in the 70s and 80s. Two storm systems moved through during the fourth week dropping 2.25 inches and 1.5 inches of rain respectively. The majority of the Arboretum's trees and shrubs handled the extreme conditions (very wet June followed by dry heat wave) quite well; we did, however, experience three "summer limb drop" events on mature oaks. Summer limb drop, also known as sudden branch drop, is a phenomenon in which seemingly healthy branches on mature trees suddenly break and drop, often on hot, still days. The causes are not fully understood, though water imbalance within the tree has been suggested.

AUGUST was dry and cool. Temperatures changed drastically from July and were slightly below average for the month. Temperatures were consistently in the mid 70s to low 80s, creating ideal summer conditions. Only once did we reach temperatures over 85°F. Sun was prevalent as only six rain events were recorded, including one large storm on the 9th that dropped 1.55 inches of rain. Evening lows were well below normal for the month.

SEPTEMBER was the second consecutive month of cool temperatures and slightly below average rainfall. We started the month with a powerful soaking storm on the morning of the 1st that dropped 1.76 inches of rain (one inch of that total fell within a one-hour period). Sunny, warm weather dominated for the next week and a half until we reached an unusually high 94°F on the 11th. The heat continued into the 12th until a storm passed through, dropping 0.88 inches of rain. The latter half of the month was unusually dry as only one supplemental rain event provided around a third of an inch of rain. High temperatures were average but low temperatures were slightly below the average. The fall equinox occurred on the 22nd, a day with cool, wet conditions.



JON HETMAN

A view of fall foliage at the Arboretum from the east side of Dawson Pond on October 10th.

Arnold Arboretum Weather Station Data • 2013

	Avg. Max. (°F)	Avg. Min. (°F)	Avg. Temp. (°F)	Max. Temp. (°F)	Min. Temp. (°F)	Precipi- tation (inches)	Snow- fall (inches)
JAN	38.7	22.7	30.7	61	2	1.65	5
FEB	37.4	23.8	30.6	50	8	6.91	32
MAR	44.1	30.0	37.1	60	19	4.95	24
APR	58.3	38.7	48.5	74	28	1.60	
MAY	69.6	47.4	58.5	93	37	4.38	
JUN	78.0	59.2	68.6	92	49	11.37	
JUL	84.7	67.8	76.3	97	59	4.15	
AUG	79.5	60.5	70.0	88	51	2.09	
SEP	72.7	51.9	62.3	94	39	3.14	
OCT	63.5	43.8	53.7	80	29	0.76	
NOV	50.3	31.9	41.1	72	16	3.29	
DEC	39.1	24.3	31.7	58	6	5.67	13

Average Maximum Temperature 59.7°F

Average Minimum Temperature 41.8°F

Average Temperature 50.8°F

Total Precipitation 50.12 inches

Total Snowfall in 2013 74.0 inches

Snowfall During Winter 2012–2013 67.6 inches

Warmest Temperature 97°F on July 19

Coldest Temperature 2°F on January 24

Strongest Wind Gust 41.8 mph on January 31

Last Frost Date 32°F on April 22

First Frost Date 32°F on October 25

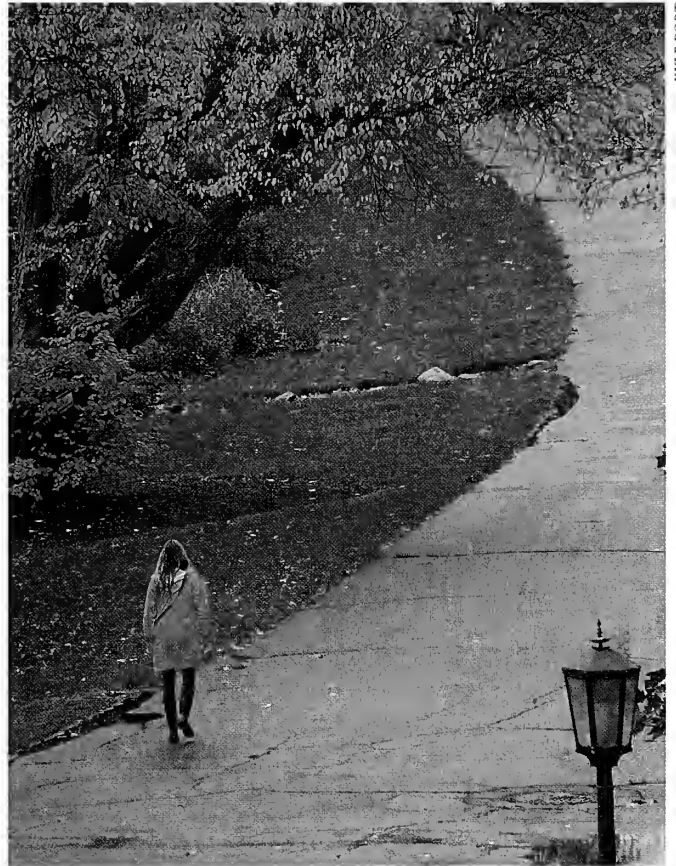
Growing Season 185 days

Growing Degree Days 2913.0 days

OCTOBER was seasonably warm and very dry. The first few days of the month were warm and sunny but turned cloudy and drizzly for the following few days. Temperatures fell throughout the month, reflecting the progressing fall season. We received a light frost on the 25th, bringing the growing season to an end. The 185-day-long growing season was nine days shorter than the previous two years and the shortest growing season over the last five years. Since the first week of the month, minimal precipitation was recorded; three events produced only 0.12 inches of rain total. This lack of rain made fall leaf pick up in the Arboretum extremely easy. Supplemental watering was necessary in certain collections, but despite the lack of rain, fall color was in full swing.

NOVEMBER was the fourth straight month with average low temperatures below the 30-year norm as we experienced colder than average overnight lows. Temperatures dipped below freezing (32°F) on 16 evenings. October's dry weather continued into November; over the first three and a half weeks of the month six rain events dropped a total of only 1.04 inches of rain, leaving the grounds parched. Over this period the water table retreated, leaving Faxon Pond almost completely devoid of water. Plants showed signs of drought stress. We received a major soaking event during the last week of the month, the first substantial rains since early September. During this stretch, an 84 day period, we received only 3.26 inches of rain.

DECEMBER was a cold month with plenty of moisture. The month started out mild and damp with temperatures in the 40s and 50s. Over the first 10 days, five separate weather events delivered rain and wet snow, accumulating 1.33 inches of rain equivalence. A cold front moved in and for the following week temperatures remained mostly below freezing as all precipitation fell as snow. Temperatures warmed again and the winter solstice on the 21st was the warmest day of the month with a high of 58°F. Two torrential downpours finished out December, dumping a total of 1.94 inches of rain. December was the fifth month in a row with below average overnight temperatures, a sign of what lay ahead.



KYLE FORT

The autumn foliage of a katsura tree (*Cercidiphyllum japonicum*, accession 882-A) along Meadow Road was color-coordinated with a visitor's jacket on a rainy November 1st.

Simply Spirea

Michael S. Dosmann

As I write on this mid-March day, a pile of thick, crusty snow lies on the ground while the sky continues to shower the Arboretum with more of the icy mess. It has been a long winter. But the longer days give me hope that spring is just around the corner and soon we will see the blooms of old botanical friends. One of these is *Spiraea prunifolia* var. *simpliciflora*, a delicate spirea collected as seed by John George Jack in 1905 during his trip to Korea (for more about this extraordinary plantsman, see the article starting on page 2 of this issue). Jack's original plant (accession 18283-A) still grows below a canopy of hickory trees along Valley Road. An earlier accession of the same species (accession 3138) came from the Royal Botanic Gardens, Kew, in 1887 and still grows in the Bradley Rosaceous Collection. This spirea is native to eastern Asia and grows wild throughout China, Korea, and Japan. Ernest H. Wilson had also collected the species in Korea, but that accession perished long ago.

S. prunifolia var. *simpliciflora* is a fine-textured shrub that functions well as a single specimen, group planting, or in the mixed border. It reaches 5 to 6.5 feet (1.5 to 2 meters) tall and at least as wide. When allowed to reach its full size, the long stems grow gracefully from the center and arch up and away to create a vase shape. Cold hardy through USDA Zone 5 (average annual minimum temperature -10 to -20°F [-23 to -29°C]), plants grow well in full sun to partial shade and tolerate most soils.

The dark green leaves are small, reaching 1 to 2 inches (2.5 to 5 centimeters) long and about ½ to ¾ inch (1.3 to 2 centimeters) wide. They somewhat resemble those of cherries (*Prunus*), which can be divined from the specific epithet *prunifolia*. The foliage develops gold to orange tones in the autumn, brightest when plants are grown in full sun.

But it is the flowers that are the most interesting part of this horticultural and botanical story. The type variety of this species is *Spiraea prunifolia* var. *prunifolia*, commonly known as bridalwreath spirea. (A type variety is the botani-

cal representative for the species and is indicated by an autonym, which duplicates the specific and varietal epithets—*prunifolia* var. *prunifolia* in this case.) Interestingly, the flowers of *Spiraea prunifolia* var. *prunifolia* are double, resembling tiny white pompons, and are produced in great quantities along the stems. This botanical variety does not represent a wild-occurring plant, but rather a horticultural oddity that is sterile, something we might now select and identify as a cultivar (cultivated variety). When Siebold and Zuccarini discovered and named the species (*S. prunifolia*) in the mid-nineteenth century they were looking at the double-flowered form, long cultivated as an ornamental in Japan. Following the protocols of plant naming, this variant became the original type variety, which meant that when Japanese botanist Takenoshin Nakai later described the plants that grow wild—those with simple, five-petaled, and fully fertile flowers—he had to give it a different varietal name: *S. prunifolia* var. *simpliciflora* (in this case, the varietal name translates literally to “simple flower”).

Though unusual, this is not the first time that a horticultural variety was designated as the botanical type. Other examples in which the species types are represented by double-flowered oddities include *Viburnum plicatum* and *Rhododendron yedoense*. In order to describe and name the single-flowered forms once they were discovered in the wild, new botanical varieties were created—*V. plicatum* var. *tomentosum* and *R. yedoense* var. *poukhanense* in these cases.

Spiraea prunifolia typically starts flowering in late April. The type variety with sterile double flowers (var. *prunifolia*) can bloom for up to three weeks, whereas the blooms on the single-flowered variety (var. *simpliciflora*) last a shorter time. This is because the petals on the fertile flowers of var. *simpliciflora* wither and drop after pollination. This spring, the blanket of white flowers on both varieties will provide a welcome change from winter's blanket of snow.

Michael S. Dosmann is Curator of Living Collections at the Arnold Arboretum.



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