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Front Cover: Sibat anak Luang, an Iban climber, worked with Peter Ashton in Sarawak. Luang stands beside a tropical chestnut (*Sterculia* sp.), an overstory tree in the mallow family (Malvaceae). Image from Arnold Arboretum Archives.

Inside Front Cover: Marian Roby Case published an annual journal, commonly known as the green book, which reported on work at her educational horticulture operation, Hillcrest Gardens. This 1922 edition was the only one without the classic green cover. Image from Arnold Arboretum Archives.

Inside Back Cover: The swamp locust (*Gleditisia aquatica,* 201-93*B) produces distinctive seedpods with a single seed inside. Photo by Jonathan Damery.

Back Cover: An American robin (*Turdus migratorius*) browses the fruits on a possumhaw viburnum (*Viburnum nudum* 'Wintertur', 431-2002*A). Photo by Matthew McDermitt.

Marian Roby Case: Cultivating Boys into Men

Lisa Pearson

Only Hillcrest farm boys, we'll soon by Hillcrest men, True and trusted citizens, we'll work for Weston then. Bound to make her greater far than she has ever been. We are the farm boys of Weston.

-FIRST VERSE OF "HILLCREST SONG"

t the turn of the twentieth century, Weston, Massachusetts, was a farming town that had become a country retreat for the well-to-do of Boston. With a commuter train connecting it to downtown Boston, less than twenty miles away, wealthy families had moved westward, searching for fresh air and rural activities. Among these estates arose an unconventional operation: an experimental farm, launched in 1910, by Marian Roby Case. For more than three decades, Case conducted the operations of a remarkable educational and horticultural enterprise called Hillcrest Gardens, which made a lasting impact on the boys who participated. In 1920, a Whitman Times article by Louis Graton described Hillcrest as "a truly philanthropic institution ... where boys, any boys, may receive, under expert tutoring, up-to-date instruction in fruit and vegetable growing. These boys are also taught the rudiments of good business. They are sent out with the truck, well loaded with the choice products their own hands have helped to raise ... to sell and thus learn self-reliance."

Marian Roby Case was born in Boston in 1864, the fourth and youngest daughter of merchant and banking executive James Brown Case and his wife Laura Lucretia Williams Case. In her youth and young adulthood, Marian and her family divided their time between their home on Beacon Street, in Boston, and their country place, Rocklawn, in Weston. After her father's death in 1907, Marian, her sister Louisa, and their mother came to live year-round in Weston. Marian had inherited about ten acres of property from her father between Wellesley and Ash Streets and proceeded to purchase other nearby plots as they became available, assembling about seventy acres of orchards and arable land over the next few years.

A Passion for Horticulture

It would seem that Marian Case had always wanted to farm, as apparently had her father. When Hillcrest was established, she initiated an annual pamphlet, known colloquially as the "green books," given the color of their covers. In the green book for 1918, she remarked, "[I] had inherited my father's love for the care and cultivation of land. How often in travelling have I seen my father wax enthusiastic over the well-tilled acres we have passed." At their Weston home, James Case had indulged in his avocation, at least during the family's summer sojourns there, by raising prize livestock for exhibition at regional agricultural fairs.

The family, whose wealth came from the dry goods business, and later banking, focused their philanthropy on organizations geared towards the improvement of society. Louisa Case was a donor to the North Bennet Street School, a training program in the manual arts located in what was then a section of Boston heavily populated with recent Italian immigrants. Marian Case was an active supporter of the Hampton Normal and Agricultural Institute, of Hampton, Virginia, through its Boston association. The institute, whose most famous graduate was Booker T. Washington, sought to educate black students to create future leaders in edu-

For more than thirty years, Marian Roby Case operated an experimental horticulture training program at Hillcrest Gardens, her farm in Weston, Massachusetts.



cation, farming, and business, and it is now known as Hampton University. Its programs stressed not only instruction in practical skills but had a deep grounding in ethical and cultural improvement.

These training programs gained traction in Boston during a nationwide boom of secular and religious progressive activism in the second half of the nineteenth century, which aimed to address, among other things, rising income inequality. Andrew Carnegie famously outlined a vision for philanthropy in an 1889 North American Review article, in which he condemned ostentatious uses of wealth and urged that charitable giving should provide training and educational opportunities for the poor. James Case, for his part, attended monthly dinners hosted by the Unitarian Club, in Boston, where speakers often encouraged the affluent attendees to use their wealth for abolishing social hierarchies.

In 1909, Marian Case's staff began preparing the land for the next year's farming season. The first eight Hillcrest boys were hired in 1910. This number steadily increased in subsequent years until it topped out at about twenty. The youngest were generally twelve years old, although occasionally some were younger. They worked half days for one dollar per week for the first two summers they were employed at Hillcrest. From the third summer and any summers thereafter, they worked full days and could earn up to twenty-five dollars per month. The pay was lower compared to other local farms, but each boy also received a new uniform every year, which looked rather like those of the Boy Scouts of America (an organization with complementary progressive ideals, which was also launched in 1910). The uniform consisted of two shirts, two pairs of pants, a Norfolk jacket, a tie, and a broad-brimmed hat. The boys also received a gift of educational enrichment more valuable than mere clothing in the form of lectures, study periods, journaling, report writing, and personal coaching on summer-long projects that fostered observational and writing skills. Case, following the model of the Hampton Institute, wanted to provide growth opportunities for the boys so they could develop into future leaders of their communities.

We know a great deal about Hillcrest from the yearly green books, which provided a thorough review of the activities on the farm each season. The publication highlighted the reports presented by the boys during their annual convocation ceremony held on Labor Day, and these were interspersed with narratives written by Case, which provide a window into her thoughts and aspirations for her enterprise. It is interesting to see the degree to which the boys' papers became longer and more detailed as the years progressed. Some of this may be due to increased coaching that Case and her assistants were giving to the boys, but it also came from Case's desire to make the green books a resource for aspiring gardeners worldwide. We see articles by the boys to which Case had her farm manager Peter Mezitt-who founded Weston Nurseries in 1923-add additional material to explain a concept or technique more fully.

Expert Instruction

The boys' days were not entirely given over to farm labor at Hillcrest; Wednesday afternoon lectures were a weekly feature of the Hillcrest program. Hillcrest boy Ernest Little described them in 1935: "One of the many advantages derived from Hillcrest Gardens is a series of instructive lectures planned by Miss Case. The program is so arranged that it includes every field of horticulture, floriculture, and botany here and abroad. They are given by leading men who are authorities in their particular line. It is with the greatest of pleasure that we welcome some of them back year after year."

The speakers, of which there were well over one hundred by the time Hillcrest ceased operations, included a number of staff members from the Arnold Arboretum: John George Jack, who in nearly fifty years at the Arboretum was an educator, plant explorer, and dendrologist; Ernest Henry Wilson, one of the greatest plant collectors of the early twentieth century; Edgar Anderson, a geneticist and public outreach coordinator; Elmer Drew Merrill, the director (initially the supervisor) of the Arboretum from 1935 to 1946; and William Judd, a longtime propagator. Other speakers included horticultural publisher J. Horace McFarland; Arlow B. Stout, a plant breeder and research scientist



Over the years, the number of boys who participated at Hillcrest Gardens each summer rose to about twenty. The 1932 participants were photographed for the annual green book.

at the New York Botanical Garden who spoke a number of times over the years on hybridizing and other aspects of plant propagation; John Caspar Wister, a longtime friend of Case who was a celebrated horticulturist and landscape designer; Edward Farrington, the editor of *Horticulture* magazine; and the Dahlia King of East Bridgewater, Massachusetts, J. K. Alexander, great-grandfather of our retired Arboretum propagator, Jack Alexander.

Beginning in 1924, Case began to invite former boys back to speak at the Wednesday lectures on their experiences in business or in higher education. Brothers Joseph and E. Stanley Hobbs spoke on their respective paths into medicine and dentistry; Edmund Mezitt, whose father Peter had been employed by Case before founding Weston Nurseries, spoke about commercial horticulture; and Charles Pear lectured on his work as a weather researcher at the Blue Hills Observatory. By bringing the so-called old boys back to lecture before a new generation, Case demonstrated the success of her pedagogy at Hillcrest; boys were indeed being cultivated into active contributors to society.

Cultivating Young Scholars

As part of the educational component of Hillcrest, the boys were expected to keep a daily journal of their work and record their observations of the plants, insects, and weather. To this end, they were each given a notebook, pencils, and drawing paper at the start of the season. They had a daily study hour during which they could research, write about their experiences, or draw. Case worked with them personally on Fridays, critiquing their reports and coaching them on their public speaking. She also enlisted a long-serving group of local educators, including Joseph Gifford, an oratory instructor from Emerson College who worked on voice training with the boys.

The summer activities culminated with the Labor Day exercises. The boys assembled and marched in carrying both the American flag and the green-and-gold flag of Hillcrest. The audience then stood for the Pledge of Allegiance, and the boys sang the Hillcrest song. Case, as mistress of ceremonies, then welcomed the guests and introduced the people who would be the judges for the boys' presentations. Each



Chen Huanyong (left) supervised the Hillcrest boys for the first ten summers. The first enrolled participant at Hillcrest was Harold Weaver (right).

of the boys read a paper they had prepared on a subject having to do with the farm. At the conclusion, the judges withdrew and chose the winners from the younger and older boys. Prizes were awarded for the papers read that day, as well as for their work in the field and in the classroom over the summer. Boys who had successfully completed one summer with distinction received a Hillcrest pin. Boys who had completed three or more summers with distinction received a pin bearing the Hillcrest motto, Semper Paratus, "Always Ready." The boys' families were encouraged to attend, and in some years, the boys were allowed to invite a girl as a guest. The subjects of the boys' papers tended to repeat from year to year. There was always a report on the Wednesday lectures, the weather, and a review of the season, which

would suggest that the boys chose their subjects from a list of topics provided by Case.

In the 1939 green book, Case thanks Charles Sprague Sargent, the late director of the Arnold Arboretum, for his support of Hillcrest, saying, "Soon after Hillcrest Gardens was started Professor Charles Sprague Sargent became interested in our work and helped us in many ways by giving us beautiful lilacs and other shrubs and trees, and by letting us go to him for advice." Sargent also persuaded Case to sponsor an essay contest for students in the Weston Public Schools. From 1921 to 1932, junior high school and high school students wrote papers on subjects suggested by Case. Unlike the summer program at Hillcrest, this essay contest was open to both male and female students, and the girls took most of the prizes over the years.

Cultivating Young Horticulturists

From the earliest days of its operations, Hillcrest's crop production was tailored to the preferences of its customers. In the 1913 green book, Philip Coburn, who had for the previous three summers conducted door-to-door sales in Weston, writes that when the seed catalogs arrived in the winter, he and Mr. Hawkins, one of Case's full-time farm employees, chose the coming season's seeds with an eye to customer favorites. During Hillcrest's first decade, direct sales were conducted in Weston and the nearby towns of Auburndale and Waltham, by horsedrawn wagon and concurrently by truck. Produce was occasionally carried as far afield as the historic Faneuil Hall marketplace in downtown Boston. By the farm's second decade, a summer stand opened in Weston near the village blacksmith on the Post Road, and doorto-door sales in town and in Auburndale were discontinued. Instead, direct marketing was concentrated in Waltham, as the dense population allowed for the best return on their efforts. Farm production catered to this primarily Greek and Italian clientele, with tomatoes, peppers, eggplant, and parsley. Sales at the market continued until 1930 when it was decided to provide Hillcrest's produce to a Weston grocer who would then handle all the cash transactions and bookkeeping.

Case was eager to trial new crops. She developed a relationship with David Fairchild of the Office of Seed and Plant Introduction at the United States Department of Agriculture and received from him new seed introductions for testing. Likewise, in 1910, Case hired Chen Huanyong (Woon-Yung Chun), a Chinese undergraduate from the Massachusetts Agricultural College in Amherst, to take charge of the boys. He worked at the farm for five seasons until 1919. Meanwhile, in 1915, Chen enrolled in the New York State School of Forestry at Syracuse University, and after his graduation he came to Harvard's Bussey Institution and studied with John Jack at the Arboretum. Chen returned to China in 1919 and later became a professor at Sun Yat-sen University. Over the years, he sent seeds for many varieties of Chinese vegetables, including eggplant, cabbage, watermelon, and bok choy, which were excitedly planted and proved popular. Seeds also came from Case's friends in Italy with whom she often wintered, including zucchini and small white eggplants.

In the present day of housing subdivisions and strip malls, it is easy to forget just how rural Weston and its neighbors, Sudbury, Wayland, Lincoln, and Wellesley, were one hundred years ago. In the early years of her enterprise, Case fretted as to whether Hillcrest was cutting into the business of other local farms. She had to strike a balance between selling their produce inexpensively but not selling it at such a low price as to undercut the other farms in town. In the 1918 green book, she wrote about discussing these issues with members of the local agricultural society: "Last spring we made thorough inquiries as to whether Hillcrest was harming the other farmers of the town and were told decidedly no. One of our well known townsmen said, 'Hillcrest is doing good work. It is interfering with nobody. Go ahead.""

The Hillcrest Boys

Initially Case limited the Hillcrest program to boys from Weston but very soon expanded it to include boys from Waltham and further afield. For the period, she was remarkably progressive in her acceptance of boys for the program, welcoming sons of old Yankee families, as well as recent immigrants from southern Italy and the eastern Mediterranean, and the son of her African American butler, George Weaver. Her mentorship, respect for, and longstanding relationship with Chen Huanyong also point to her progressive ideals. In an age when children were to be seen but not heard, Hillcrest boys were encouraged to speak and make their opinions known. In fact, as Case said in 1922, "There is no sectarian or political influence exerted at Hillcrest Gardens; each boy has a right to his opinion, whether we agree with him or not."

Harold Weaver, the first boy enrolled at Hillcrest, participated for six seasons. He was also the first of the Hillcrest boys to go to France, in 1918, with the American Expeditionary Forces of World War I, as part of the 369th Infantry Regiment, the all-black unit nicknamed the Harlem Hellfighters. Case published an excerpt

de Miss Marion Roby Case cow Devoto affectio offre risjettosamente ed eternamente memore 5 figlio italiano Vincenzo Buiocco Napol, 19 Liglis, 1929 VIE

Case was photographed by Vincenzo Ruocco, in Naples, Italy, in 1929.

from a letter he wrote from "somewhere in France," in which he said, "You do me honor, Miss Case when you tell me that I am the first Hillcrest Boy to come to France. My Hillcrest pin is ever with me on the lapel of my blouse. I often look at it and think how I should dislike to lose it in No Man's Land and how I hope to bring it safely from No Man's Land to Weston again so that you yourself may see the pin that has travelled 4,000 miles." Case went on to name two other students who were serving in the military: one as an aviator in Texas, the other in the Marines. Weaver was commissioned a second lieutenant in France, perhaps due in part to the leadership skills he learned at Hillcrest. He and the other Hillcrest boys in uniform all returned safely from their service in the armed forces at the close of the war.

Case never married and had no children of her own, but she nevertheless became a second mother to about one hundred Hillcrest boys whom she guided firmly but lovingly. In 1923, she reflected on her satisfaction in one of the boy's papers, noting that his "tribute is very pleasing to one who has tried to mother the boys, and who through a long life has seen mistakes which she feels that the training in sturdy independence, responsibility, individuality and co-operation which the boys have at Hillcrest Gardens may help to overcome." The loving regard with which Case was regarded by the Hillcrest boys is clear in their writings and later reminiscences. Case seemed to inspire affection wherever she went. She was photographed by a friend, Vincenzo Ruocco, in Naples, Italy, in 1929, and he inscribed the picture, "A Miss Marian Roby Case madre americana, con devoto affetto offre rispettosamente ed eternamente memore il figlio italiano." The note roughly translates to, "To Miss Marian Roby Case, American mother, offered with devoted affection, respectfully and eternally, from her Italian son."

Transitions

As Case became older, she began to cast about for a successor organization to take over Hillcrest. She considered the Massachusetts Horticultural Society, the University of Massachusetts, and other organizations, settling upon the Arnold Arboretum in 1942. The Hillcrest property was acquired by the Arboretum through bequests and donations by Case and her sister Louisa that occurred between 1942 and 1946. It was renamed the Case Estates and consisted of the family homestead, Rocklawn, and additional parcels of land and buildings acquired by Case. As part of the Arboretum, the property's main function was to provide additional nursery space for our living collections and to serve as a horticultural experimentation area. Weston's colder temperatures meant that plants that proved hardy there would definitely be hardy in the more temperate climate of Boston. In the 1950s and 1960s, experimental plantings and trial gardens were introduced to show plants, including herbaceous material, which would be appropriate for suburban home landscapes. The Case Estates buildings provided housing for staff and space for educational programs and public events. Case's will did not impose any restrictions on her bequests to the Arboretum, and she realized that, as times changed, the Arboretum might desire to sell the property, in which case she directed that the proceeds of the sale should be added to the general endowment. This outcome occurred in 2017 when the remainder of the property was sold to the town of Weston.

In creating an educational work program for boys, Case sought to encourage future farmers, as well as leaders in whatever field a boy chose to pursue as his life's work. Women might well ask why she did not extend this program to girls. The answer is in the social mores of the era in which Hillcrest was conceived. In 1909. women were only starting to make their way into the public sphere, and it would have been very unusual for mixed groups of girls and boys to work together doing farm labor outside of a home situation. This was the era when school entrances had separate doors for boys and girls. Case grappled with what work was appropriate for the younger boys finding that the heavier farm labor was too much. Times, however, were changing. The progressive forces that inspired programs like Hillcrest were complemented by advocacy for women's rights, which extended beyond the right to vote. Pioneering women, especially the "farmerettes" of the Women's Land Army in Britain and the United States during World War I, led the change, and Case knew that a female horticulturist could be the match of any man.

"Sometimes I feel as if I would like to have a woman take care of my flower garden at Hillcrest," she wrote in Horticulture magazine in 1920. "For as a rule women are better nurses. Men are good for spring and autumn work. They can plant, do good landscape work, go in for effects. But when it comes to the care that plants need in summer, the watching, nursing and babying I believe that women will prove better." She went on: "There are some men who have this woman element to a large degree—not the feminine, there is a difference-of them, poets, artists and good gardeners are made. The marking of crosses on a piece of paper is not going to make any difference in the spirit of womanhood in either man or woman and there is still truth in the old saying that the hand that rocks the cradle is the hand that rules the world."

Lisa Pearson is head of library and archives at the Arnold Arboretum. Her book *Arnold Arboretum* was published as part of the Images of America series in 2016. She had the pleasure of meeting two of the "old boys" from Hillcrest Gardens, Jack and Tom Williams, about fifteen years ago. They both spoke of Case in affectionate terms.



The Viburnum Lentago Clade: A Continental Radiation

Elizabeth Spriggs

'arrived at the Missouri Botanical Garden's herbarium in the middle of a summer after-**L**noon in 2014. I had spent the past two days driving and looking for Viburnum in the farm country of northern Illinois where occasional natural populations can be found in wooded roadside ditches. I was a second-year graduate student at Yale University, and it was my second collecting trip. This herbarium was an important destination because it is the second largest in the United States, and it has excellent collections of North American plants. I was planning to photograph all the viburnum specimens. I especially wanted to learn how to identify the seven viburnum species that taxonomists have traditionally grouped in the Lentago clade. A curator met me and took me to the viburnum section, where he showed me five full floor-to-ceiling cabinets. As I began to sort through the specimens that afternoon, I was totally overwhelmed: there were far too many to photograph, and I couldn't tell the species apart.

The Viburnum Lentago clade is a small lineage of wide-ranging shrubs and small trees that are common in woodland edges of North America. Two members of this clade, nannyberry (V. lentago) and witherod viburnum (V. cassinoides), occur in New England and the upper Midwest. The lineage also includes the blackhaw (V. prunifolium), rusty blackhaw (V. rufidulum), and possumhaw viburnum (V. nudum), which have more southern distributions. Walter's viburnum (V. obovatum) occurs primarily in Florida, and V. elatum is restricted to Mexico. The species in this lineage all flower in the early spring and produce large blue or black bird-dispersed fruits.



One of the most notable features of the group is that its members look very similar to one another, and nearly all the traits that distinguish the species are subtle. After my first day at the herbarium, I reread the two best treatments of the Lentago clade: Thomas Jones's 1983 graduate thesis and Waldo McAtee's A Review of the Nearctic Viburnum. Both taxonomic keys are full of equivocal phrases like "leaves usually short-pointed or rounded apically," "petioles more or less crinkly-margined," and "veins less scurfy, usually glabrous." Resigned to the fact that I might not be able to tell the species apart, I decided to photograph as many specimens as I could with the hope that I would be able to figure them out once I was back in New Haven.

Over the next couple of years, I spent many weeks collecting viburnums from wild populations in the eastern United States, collecting 330 individuals. I spent many more weeks looking at herbarium specimens. I did eventually learn to tell the species of the *Lentago* clade apart. Many botanists know the feeling: familiar species become easy to identify, but it is almost impossible to describe what is distinctive about them. Once I knew the species, I understood the reason for ambiguous descriptions in the taxonomic keys. My own ways of identifying the species are just as difficult to describe—like picking out friends in a crowd of people.

This detailed work on a small plant lineage led to surprising results and new insights into the biology of the clade. We even rediscovered a species, *Viburnum nitidum*, in the southeastern United States, which has been ignored for most of the past two centuries. It turned out that a lot can be learned from a group of plants that was known even to Linneaus, a lineage collected hundreds of times and studied by generations of taxonomists.

History of the Clade

Although most viburnums today occur in temperate or boreal environments, phylogenetic evidence suggests that the ancestors of *Viburnum*, and of the *Lentago* lineage specifically, lived in the warm temperate forests of Asia. Then, around thirty to thirty-five million years ago, *Lentago* moved into North America

Taxonomists show the evolutionary relationships between species using phylogenetic trees. Here, a tree for *Viburnum* species in the *Lentago* clade reveals two primary subgroups: Species in the core *Lentago* clade, like *V. prunifolium* (left), produce flowers and fruit in unstalked clusters. Species allied with *V. nudum* (above) are borne on stalks.

(Landis et al., *in prep*). The only close relatives of the *Lentago* clade are *V. punctatum* and *V. lepidotulum*, which both live in warm forests in Southeast Asia, many thousands of miles of away. Because no closely related species occur in Europe or Northern Asia, it is impossible to be sure how the *Lentago* clade's ancient migration occurred. Researchers, however, have found a fossilized viburnum pollen grain in Iceland, which has distinctive characteristics typical of species in the *Lentago* clade. This suggests that *Lentago* was likely present in Iceland about fifteen million years ago and may have migrated to North America through Europe, over the North Atlantic Land Bridge (Landis et al., *in prep*).

Once in North America, the *Lentago* clade split into two lineages: the core *Lentago* clade and the Viburnum nudum species complex. The core Lentago includes five species: V. lentago, V. prunifolium, V. rufidulum, V. obovatum, and V. elatum. The V. nudum species complex is a small, variable lineage, which I'm calling a "species complex" because when I started working on it, there was a lot of uncertainty about how many species were included and how they were different from one another. Like most of *Viburnum*, the species in this complex bear fruit on stalked inflorescences (umbel-like compound corymbs), but in the core *Lentago* clade, the inflorescences are sessile or unstalked, which means that leaves are produced immediately under the inflorescence branches. Each of these two lineages has radiated into habitats that today span the range of eastern North America from central Florida to Nova Scotia.

Wild Hybridization

One of the most enigmatic species of the *Lentago* clade is the blackhaw, *Viburnum prunifolium*. This species occurs in a geographic area that overlaps with both *V. lentago* and *V. rufidulum*, and it is intermediate between them in many traits. Joe Brumbaugh and Arthur Guard, who observed the overlapping ranges of all three species in Indiana, concluded, in 1956, that repeated backcrossing between these species—a process known as introgression—could be a significant cause of taxonomic confusion. Botanist Linda Rader went further and argued, in 1976, that *V. prunifolium* might actually be a hybrid species formed by an ancient

hybridization event between *V. lentago* and *V. rufidulum* parents. Although *V. lentago* and *V. rufidulum* do not come in contact today, it is reasonable to imagine that they might have shared a geographic range in the past and might have had opportunities to hybridize.

Each of these theories about hybridization is supported by the fact that hybrids among the species are possible. The cross between Viburnum lentago and V. prunifolium is known as $V_{\cdot} \times jackii$. Alfred Rehder, a taxonomist who worked at the Arnold Arboretum for much of his career, proposed the name in honor of his colleague John George Jack, who, in 1908, noticed plants in the Arboretum that appeared intermediate between V. lentago and V. prunifo*lium* and assumed that they were spontaneous hybrids. Although those individuals are no longer at the Arboretum, a specimen of V. × jackii growing at the Morton Arboretum was obtained from the Arnold Arboretum and is likely to be from the same original lineage.

The only documented set of controlled crosses between Viburnum lentago and V. prunifolium was carried out by Donald Egolf, a graduate student at Cornell University who would become a leading research horticulturist at the United States National Arboretum. His findings, in 1956, found that a cross between V. lentago and V. prunifolium yielded twentyeight seeds and twenty-six plants, roughly the same number as crosses between only V. lentago. These numbers are surprising because they suggest that intrinsic barriers that could prevent hybridization are very low for this species pair: if an insect transported pollen from V. lentago to a V. prunifolium flower, the V. pruni*folium* would likely produce fertile seeds. All of this indicates that hybridization is possible and could even be common in natural populations where both species occur.

In order to test for hybridization and get a better understanding of these species, I went on a series of road trips to collect leaf samples from across the range of *Viburnum lentago*, *V. prunifolium*, and *V. rufidulum*, including areas where multiple species occur. At each natural population, I collected leaves to use for morphological measurements and leaves to use for DNA extraction and sequencing. Across all of these areas, I found no evidence of hybrid zones or



The overlapping ranges for three species in the core *Viburnum Lentago* clade raise questions about how these species remain distinct. Shown with *V. lentago* in blue, *V. prunifolium* in yellow, and *V. rufidulum* in green.

of widespread gene flow among species. While the species sometimes appear morphologically similar to one another, it turned out that this variation is not related to genetic structure or hybridization. That is, in cases where *V. rufidulum* looked somewhat like *V. prunifolium*, genetic sequencing showed that it was still 100 percent *V. rufidulum*. Overall, our sequencing found that *V. prunifolium* did not originate through hybridization. Instead, *V. prunifolium* is sister to the southern *V. rufidulum*, and the northern *V. lentago* is a more distant relative (Eaton et al., 2017; Spriggs et al., 2019).

Out of all the 180 individuals sequenced, only two appear to be admixed (have genes from two different species). These two individuals are from a small population in northern Kentucky where *Viburnum prunifolium* and *V. rufidulum* occur together in a rocky roadside woodland, five miles east of the Kentucky River. These individuals were morphologically similar to *V. rufidulum* (I labeled them as *V. rufidulum* when I collected them), but when sequenced, they appeared to be half *V. prunifolium* and half *V. rufidulum*.

Floral Timing

Whenever hybridization is possible but rare, it suggests that something is acting to prevent or eliminate hybrids, in other words, mechanisms of reproductive isolation. Hybridization in natural populations has several possible outcomes. One possibility is that hybridization between two species will be so common that the species will eventually merge to become a single species. At the other extreme, if hybrids between two species are unfit, natural selection can cause species to evolve ways of avoiding one another. In some plant lineages, closely related species have different numbers of chromosomes, often leading to inviable offspring. Another common way plants avoid interbreed-



Flowering time may explain why few natural hybrids occur between *Viburnum prunifolium* (left) and *V. rufidulum* (right). The author photographed both species on April 27, 2015, in Indiana. These temporal differences were later supported by analysis of herbarium specimens, which revealed a nine- to ten-day difference between flowering times for these closely related species.

ing is with flowers that evolve to attract different pollinators. In the *Lentago* clade, however, the species have the same number of chromosomes (Egolf, 1956), and their flowers are extremely similar (Donoghue, 1980).

How, then, do these species in the core *Len*tago group maintain their separation? The answer seems to lie in subtle habitat differentiation and phenological timing. Brumbaugh and Guard, in 1957, described habitat distinctions for the three overlapping species based on their work in Indiana: "V. lentago occupies poorly drained areas; V. prunifolium, moist borders of woods, and V. rufidulum, dry rocky slopes." This characterization matches my own experience in the field, although I have also found that it is not difficult to find areas with two or more of the species occurring together. This kind of habitat differentiation could decrease how often the species flower in close proximity to one another. If the species are also adapted to slightly different habitats, hybridization might be disadvantageous because it could separate beneficial traits or cause beneficial traits to be lost altogether.

Even more intriguing, several authors who have observed these species in the field or at arboreta sometimes mention offset flowering times. Viburnums typically flower once a year for only ten to fourteen days, and flowering time is often very synchronized within species (Donoghue, 1983). Rehder, in 1920, wrote that Viburnum prunifolium flowers about a week before V. lentago, and Rader, in 1976, noted that V. prunifolium flowered about two weeks before V. rufidulum. My doctoral advisor Michael Donoghue observed this same pattern, where V. prunifolium flowers about a week ahead of the other two species, while he was conducting his own dissertation research at the Arnold Arboretum (Donoghue, 1980). To investigate whether flowering time varies between the species in wild populations, I drove through Ohio, Indiana, and Kentucky in the early spring of 2015. In this region, V. prunifolium was very common and V. rufidulum less so, but over the course of a week, I found multiple populations of each species and consistently found V. prunifolium in full flower while V. rufidulum had green buds.

Anecdotal evidence from single locations (even wild populations) is helpful but not all that convincing because each of these species occurs across a large geographic area, and each year populations experience a variety of climate conditions. To try to understand patterns of flowering time, I used herbarium specimens, which were excellent because the species are relatively common and have been collected hundreds of times from across their ranges. Even more importantly, most specimens are reproductive, meaning they have flowers or fruits, so we found plenty of suitable material, representing a large number of years. With the help of Caroline Schlutius, an undergraduate researcher, I found 1,379 flowering specimens that spanned the range of each of the species.

By examining these specimens, we found clear geographic patterns in flowering time and consistent differences in flowering between species. First, we found that within each species, southern populations in warmer climates flowered earlier than northern populations in colder climates. More surprisingly, we found small but consistent differences in flowering time that remained remarkably constant across the regions where species co-occurred. In any given location, a nine- to ten-day difference in flowering time occurs between species, with a sequence that matches previous observations-Viburnum prunifolium flowers before V. lentago and V. rufidulum. Because viburnums only flower for ten to fourteen days total, this small offset can dramatically decrease the opportunities for pollen transfer among plants. To be clear, these findings do not suggest that all of the individuals will flower in sequence every year in every location, only that in any given place for a particular year, the majority of individuals of one species will flower ahead of the majority of individuals of the other.

Hidden in Plain Sight

A second major focus of my work on the *Len-tago* clade was the *Viburnum nudum* species complex. For the *V. nudum* complex, I wanted to sort out how many species there are, where they occur, and whether any traits consistently differentiate the species. In my first year collecting viburnums, I started in Florida and drove north. I was specifically targeting

the *V. nudum* species complex, but it was very hard to find. I was surprised because viburnums are easy to find in New England, and I had expected to encounter populations driving down sideroads or in the state parks where I had permits to collect. This was not the case, and for future trips, I researched locations extensively using herbarium specimens and talking with local botanists.

The first year, I collected a couple of individuals near Gainesville and then didn't find V. *nudum* again for a full week. The populations I had collected in Florida were in sandy soil along shallow streams, and I was looking for similar habitats as I made my way up the East Coast. I was driving on a small road along the edge of a black-water swamp in coastal South Carolina when I found the next population. A small group of viburnums was strung out along the edge of the road, several inches deep in muddy water, near a swamp with bald cypress (Taxodium distichum) and water tupelo (Nyssa aquatica). Not only was this a totally different environment than I was expecting but the plants looked different. The Gainesville plants had seemed delicate: they had small, narrow leaves, and the inflorescences bore bright pink and more mature black fruits simultaneously. This South Carolina population had thick leaves, larger than my hand, and pale green fruits. After several more collecting trips over the next several years, allowing us to sequence individuals from many populations, we discovered that these habitats are both typical for the V. nudum complex, but they contain totally separate genetic lineages, each adapted to its own environment.

These results were surprising because they are at odds with the generally accepted taxonomy of *Viburnum nudum* species complex, which dates to the eighteenth century. Linnaeus described *V. nudum* in the first edition of *Species Plantarum*, published in 1753, and added *V. cassinoides* in the second edition, in 1782, distinguishing *V. cassinoides* by its leaf shape. Then, in 1789, William Aiton, the first director of the Royal Botanic Gardens, Kew, proposed two additional species, *V. nitidum* and *V. laevigatum*. Since then, more than eight other names have been proposed for segregates within the complex (McAtee, 1956), but none



As the author dug into the puzzling taxonomy of the *Viburnum nudum* complex, fieldwork revealed that the plants occurred in three distinct habitats. Most surprisingly, those in sandy soils in Florida (above) proved to be a long overlooked species, *V. nitidum*.

of these have been widely recognized. In recent floras, only two species or subspecies are recognized: *V. cassinoides* in the North and *V. nudum* in the South (Jones, 1983; Small, 1933; Gleason and Cronquist, 1991; Ferguson, 1966; Radford et al., 1968; Strausbaugh and Core, 1978; Weakley, 2012).

When we sequenced DNA of eighty individuals, we found three different lineages in the Viburnum nudum species complex, all of which seem to be evolving independently. Most importantly, we found that the way V. nudum is typically described makes it paraphyletic, meaning that the name refers to a partial evolutionary lineage. The oldest genetic split in the V. nudum complex lineage is not between the northern and southern populations (traditionally V. cassinoides and V. nudum). Instead it is between the large-leaved populations that occur in swamps and the rest of the complex (including sandy stream populations and northern populations). Our genetic data show that each of these three lineages is distinct and evolving independently, and therefore all three deserve to be recognized as species (Spriggs et al., 2018). Linnaeus's V. nudum matches the large-leaved species that occurs in swamps; V. cassinoides corresponds to the northern species in our analyses; and the sandy-soil species seems to match Aiton's V. nitidum.

After surveying herbarium specimens from across the Southeast, we determined that *Viburnum nitidum* is mostly restricted to the coastal plain. From Florida it extends up to North Carolina, along the coast and in the Sandhills region, then west into the eastern edge of Texas. *V. nudum* is more widespread and occurs throughout the coastal plain and the Piedmont, from Delaware to Arkansas. The habitats of these two species are interdigitated across the Southeast, and the species occur in close proximity to one another frequently yet remain distinct and do not hybridize.

Our findings support recent arguments that the flora of the North American Coastal Plain is under-described, meaning it is more diverse than the current taxonomies suggest (Sorrie and Weakley, 2001; Noss et al., 2015). It seems that this disregard was not always the case. Over the past century, field botanists, particularly southern botanists like William Ashe, of North Carolina, or Alvan Chapman, who spent most of his career in Georgia, recognized subtle variation in the habitats of the coastal plain and described many species. These proposed species have been systematically ignored or lumped into larger widespread "species" that may turn out to be paraphyletic. Genetic sequencing may vindicate at least some of these descriptions, as was the case for Aiton's *V. nitidum*.

Significance of this Clade

It is reasonable to question whether it is important to know how many species are in the *Lentago* clade or to know how exactly they are related to one another. If *Viburnum nitidum* is very similar to *V. nudum*, does it really matter that it has a separate name? Is it useful to know whether *V. prunifolium* originated as a hybrid species? Does knowing the recent evolutionary history of these species have any broader implications? I believe that all this lineage-specific knowledge about species limits, occurrences, and history is important for conservation and also provides insight into the ecology and evolution of North American forests.

For one thing, species identities are fundamentally important because they affect how species are recognized and valued, and whether they are conserved. Some might view the long list of proposed (and subsequently ignored) botanical names for segregates of the Viburnum nudum complex as wasted effort, but I view these names and descriptions as essential contributions, stepping-stones leading along a path to accurately characterize plant diversity. The numerous common names for V. nudum, including witherod viburnum, possumhaw, wild raisin, and Appalachian tea, suggest that even nontaxonomists knew these plants and attempted to differentiate them. With genetic sequencing, we have new opportunities to get this right, to rigorously test species limits so that the current names and species descriptions are accurate. This is especially important because relatively few plant lineages in North America (or elsewhere) have been studied with fine-scale genetic sequencing, and there is much to learn.

Accurate species descriptions are also an essential starting point for ecological studies that seek to understand species distributions or interactions. If Viburnum nitidum and V. nudum are considered as a single entity, their distribution might be confusing or bimodal because it would include two very different habitat types. If, instead, V. nitidum is considered alone, its habitat preferences would likely be much more specific, and it might even be a useful indicator species that could serve as a quick way to identify a particular habitat or plant community. Similarly, species often differ for traits that are not readily apparent to human observers, and these can be critical in shaping interactions with insects or other species. Imagine, for instance, that there was reason to suspect that V. nitidum was a host species for a rare caterpillar, but in an assessment of this relationship, a researcher sampled V. nudum thinking it was the same as V. nitidum. This kind of mistake could lead to inconsistent or misleading results. Species are an essential unit for many ecological studies, and when species descriptions are inaccurate, there can be significant consequences.

Finally, understanding the evolution of this small lineage can provide important insights into the evolution of the North American flora more generally. Each of the two major lineages of the Lentago clade diversified in eastern North America over many millions of years, and each lineage has differentiated into a series of morphologically similar but ecologically distinct species. Similar patterns of slow diversification into subtly different species are also apparent in other North American lineages like maples (Acer), dogwoods (Cornus), or ash (Fraxinus). Our work showed how the species of the *Lentago* clade have persisted through climate fluctuations associated with glaciation and provided evidence on one of the mechanisms (flowering time) that these species use to maintain their separation. Tensions around species identifications have hindered our understanding of the Lentago clade for over a century, but after years of observation in the field and extensive genetic sequencing, the species that had seemed incomprehensible to me at the



Taxonomic research reveals that all plants—even common garden denizens like *Viburnum cassinoides* (above)—provide a record of millions of years of plant evolution.

Missouri Botanical Garden herbarium became clear. Many other plant lineages that form the foundation of the flora of eastern North America likely have similar histories of subtle differentiation and persistence, promising countless stories waiting to be revealed.

References

- Brumbaugh, J. H. and A. T. Guard. 1956. A study of evidence of introgression among Viburnum lentago, V. prunifolium, and V. rufidulum based on leaf characteristics. Proceedings of the Indiana Academy of Sciences, 66: 300.
- Clement, W.L., and M.J. Donoghue. 2011. Dissolution of Viburnum section Meaglotinus (Adoxaceae) of Southeast Asia and its implications for morphological evolution and biogeography. International Journal of Plant Sciences, 172: 559–573.
- Clement, W.L., M. Arakaki, P.W. Sweeney, E.J. Edwards, and M.J. Donoghue. 2014. A chloroplast tree for *Viburnum* (Adoxaceae) and its implications for phylogenetic classification and character evolution. *American Journal of Botany*, 101: 1029–1049.
- Donoghue, M.J. 1980. Flowering times in Viburnum. Arnoldia, 40(1): 2–22.
- Donoghue, M. J., B. G. Baldwin, J. Li, and R. C. Winkworth. 2004. *Viburnum* phylogeny based on chloroplast *trnK* intron and nuclear ribosomal ITS DNA sequences. *Systematic Botany*, 29: 188–198.
- Eaton, D. A. R., E. L. Spriggs, B. Park, and M. J. Donoghue. 2017. Misconceptions on missing data in RADseq phylogenetics with a deep-scale example from flowering plants. *Systematic Biology*, 66(3): 399–412.
- Egolf, D. R. 1962. A cytological study of the genus Viburnum. Journal of the Arnold Arboretum, 43(2): 132–172.
- Egolf, D. R. 1956. Cytological and interspecific hybridization studies in the genus *Viburnum* (Unpublished doctoral dissertation). Cornell University, Ithaca, NY.
- Ferguson, I.K. 1966. The genera of Caprifoliaceae in the southeastern United States. Journal of the Arnold Arboretum, 47(1): 33–59.
- Gleason, H. A. and A. Cronquist. 1991. Manual of vascular plants of Northeastern United States and adjacent Canada (2nd ed.). Bronx, NY: New York Botanical Garden.
- Jones, T. H. 1983. A revision of the genus Viburnum section Lentago (Caprifoliaceae) (Unpublished doctoral dissertation). North Carolina State University, Raleigh, NC.

- Landis, M. J., D. A. R. Eaton, W. L. Clement, B. Park, E. L. Spriggs, P. W. Sweeney, E. J. Edwards, and M. J. Donoghue. In prep. Joint estimation of geographic movements and biome shifts during the global diversification of *Viburnum*.
- McAtee, W.L. 1956. A review of the Nearctic Viburnum. Chapel Hill, NC: Author.
- Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, and R.K. Peet. 2015. How global diversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distribution*, 21: 236–259.
- Rader, L. L. 1976. A biosystematics study of *Viburnum* prunifolium and *Viburnum* rufidulum (Caprifoliaceae) (Unpublished M. S. dissertation). University of Tennessee, Knoxville, TN.
- Radford, A.E., H.E. Ahles, and C. Bell. 1968. Manual of the vascular flora of the Carolinas. Chapel Hill, NC: The University of North Carolina Press.
- Rehder, A. 1920. New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. *The Journal of the Arnold Arboretum*, 2(2): 121–128.
- Small, J.K. 1933. *Manual of the Southeastern Flora*. New York: Author.
- Sorrie, B. A. and A. S. Weakley. 2001. Coastal plain vascular plant endemics: phytogeographic patterns. *Castanea*, 66: 50–82.
- Spriggs, E. L., C. Schlutius, D. A. R. Eaton, B. Park, P.W. Sweeney, E. J. Edwards, and M. J. Donoghue. 2019. Differences in flowering time maintain species boundaries in a continental radiation of *Viburnum. American Journal of Botany*, 106(6): 833–949.
- Spriggs, E. L., D. A. R. Eaton, P. W. Sweeney, C. Schlutius, E. J. Edwards, and M. J. Donoghue. 2018. Restriction-site-associated DNA sequencing reveals a cryptic Viburnum species on the North American Coastal Plain. Systematic Biology, 68(2): 187–203.
- Spriggs E. L., W. L. Clement, P. W. Sweeney, S. Madriñán, E. J. Edwards, and M. J. Donoghue. 2015. Temperate radiations and dying embers of a tropical past: the diversification of *Viburnum*. *New Phytologist*, 207(2): 340–354.
- Weakley, A.S. 2012. Flora of the Southern and Mid-Atlantic States. Retrieved from http://www. herbarium.unc.edu/flora.htm

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Resolving the Enigma of Rainforest Biodiversity

Peter Ashton

berdeen, Scotland, as it was when I arrived as a professor, in 1966, at the cusp of the North Sea oil bonanza, was a very different coastal town from those in Brunei and Sarawak, where I had been based for eight of the previous ten years, while conducting fieldwork in the rainforests of Borneo. At 57° north latitude, the summer skies in Aberdeen never completely darken and native tree species are few, but the University of Aberdeen had a long tradition of research and instruction in tropical agriculture, including tea and rubber. As a new professor, I found colleagues with common interests, who shared my enthusiasms and encouraged me to continue in my research. A central puzzle had grown in my mind: How can so many species of giant sessile organisms-rainforest trees-apparently coexist in

stable mixture and how did these communities originate?

Elmer Merrill, celebrated botanist of East Asian floras and director of the Arnold Arboretum from 1937 to 1946, reasoned that the extraordinary species diversity of tropical and warm temperate forests in East Asia suggested an origin there for all flowering plants. Paleontological research and the growing science of molecular phylogeny would ultimately indicate the reverse-suggesting that the Aisian tropics were primarily devoid of broadleaf evergreen rainforests until the current tree families invaded in more recent evolutionary historyyet the warm, wet equatorial climate of the tropical Far East appears, nevertheless, to be optimal for tree growth and survival. Around 4,500 plant species are known to occur in northern Borneo.

Understanding how rainforest tree species sustain a stable mix within their communities and why these communities vary in species diversity was more than theoretical interest: If species are distributed at random within their soil-defined communities, how could consistent and predictable protocols for silvicultural management following timber harvesting be devised?

At the time, research in temperate ecosystems was revealing that populations of tree species were remarkably genetically variable. This was the opposite of the widespread assumption that, for rainforest trees in species-diverse communities, self-pollination would prevail, resulting in low genetic variability within populations. As Charles Darwin foresaw, natural selection depends on the existence of diversity, which we now know to be genetic and heritable. Genetic uniformity within populations would imply lack of selection and suggest that species sharing the same habitat are ecologically complementary, surviving together through the random consequences of their seed dispersal. We decided to adopt a broad approach to explore these issues, combining crosspollination experiments with comprehensive observation of the reproductive biology of selected species, tracking them from bud formation to seed dispersal. We would bag the flowers after carefully brushing pollen onto the stigmas and then examine the genetic consequences of these crosses, comparing the genetic variability of the seedlings to the variability sampled among trees in the broader population.

This research came with formidable challenges: the first was to find a safe way to ascend a 150-foot (45-meter) tree to its outer twigs in order to manipulate cross-pollination using a squirrel-hair artists brush. We were fortunate from the start. The North Sea oil was beginning to flow. I found an enterprising oilfield engineer who would work with me to devise a means of reaching the flowers through tree prosthesis: Three telescoping aluminum alloy booms, each 15 feet (4.6 meters) long, which were light enough to be carried into the forest to a tree about to flower. Combined with a cable, ropes, a simple manual dockside winch, and a boatswain's chair, the booms allowed a researcher to be lifted to the place of operation. But who among us academics, approaching middle age, would volunteer? The solution was obvious: find some students! So it was that I managed to write a persuasive grant proposal to an independent foundation created by the Unilever Corporation, from which I succeeded in gaining the necessary support. Six graduate scholarships were awarded for Malaysian students who had the necessary combination of fieldwork interest and some experience, curiosity, scientific acumen, and derring-do. Three women and three men were selected.

Each student variously focused on the reproductive biology of both an emergent and a subcanopy tree species. Fieldwork was carried out at the Pasoh Forest Reserve, in central Peninsular Malaysia, about one hundred miles southeast of the capital city, Kuala Lumpur. At that time, the pollinators of dipterocarps-trees in the family Dipterocarpaceae, which dominate the overstory of these rainforests-were unknown. But in the second year, student Chan Hung Tuck collected inflorescences from a tree, sealed them in a plastic bag, and took them back to his lab at the university. To his amazement, when he opened the bag the following morning, he found several tiny insects and holes in the buds from which they had apparently escaped: thrips. Another student, Simmathiri Appanah, immediately got to work, dangling sticky plastic bottles in the canopy to trap insects. Together, their work confirmed that thrip eggs were laid in the flower buds and that thrip populations increased day by day as the dipterocarps developed buds en masse. When the open corollas fell to the ground beneath, a haze of tiny organisms was released, the insects batting their oar-like wings in the humid air. Petals are one of the very few plant organs not chemically defended in the rainforests, so they are like vegetarian McDonald's hamburgers sustaining rainforest insect diversity.

The genetic work yielded unexpected results as well. The Pasoh population of the dipterocarp *Shorea leprosula*, by then the chosen emergent

Graduate student Chan Hung Tuck uses a custom-designed boom to perform cross-pollination experiments in the canopy of *Shorea leprosula*.



Ashton's research plot at the Pasoh Forest Reserve became one of sixty-seven sites in the Center for Topical Forest Science, now known as the Forest Global Earth Observatory (ForestGEO). Sites in Southeast Asia and southern East Asia are marked in green.

for all our research, proved to have a genetic structure remarkably similar to the average temperate broadleaf canopy tree, with variability relatively low among neighboring trees but increasing to a population average at a radius of about 330 feet (100 meters). This is consistent with the maximum usual distance of dispersal of the winged dipterocarp fruit and the possible distance that thrips might be wafted by daily air turbulence within the sunny forest canopy. Later studies by others have confirmed that this phenomenon is close to the general rule, although some emergent dipterocarps and trees in other families attract pollinators that forage over long distances. Examples we examined included tree species visited by the giant Asian honey bee (Apis dorsata) and others visited by a cave-roosting, nectar-feeding bat (Eonycteris spelaea). Many of these same tree species bear large comestible fruit, the seeds of which are dispersed by mammals and large birds. It was becoming clear, however, that a preponderance

of minute, small-winged pollinators, wafted aloft between distant conspecific individuals in the forest cornucopia, was maintaining genetic diversity across widespread habitats.

Critically important, Robert MacArthur and my future Harvard colleague Edward O. Wilson had shown, in their 1967 book, The Theory of *Island Biogeography*, that animals on islands accumulate species at rates of immigration and extinction that vary with the area of the island: an increase of area by 90 percent is required to double the size of a fauna. Dipterocarps, however, did not follow these predictions. Whereas the large island of Sumatra includes just over 100 dipterocarp species, there are 158 species in Peninsular Malaysia, only one quarter of the area, while Borneo, one and one half the area of Sumatra, contains 270 species. The overall tree floras are consistent with these figures. As a consequence, the relationship between the number of motile organisms-animal speciesand the land masses they occupy, predicted by



Ashton operates the boom equipment at the Pasoh Forest Reserve.

MacArthur and Wilson, are rarely achieved by plants, especially trees, on account of the diversity of soils within which species are confined by interspecific competition.

I joined the staff of the Arnold Arboretum in 1978, and my time as director was, for a while, fully occupied with pressing issues at Jamaica Plain. But in 1982, I attended a meeting on tropical forest ecology with my former Aberdeen student Ian Baillie, a tropical forest soil scientist. We presented a paper showing how soil nutrients governed forest community composition at topographic and geologic spatial scales in lowland Borneo. I had, by that time, become convinced that tree species in hyperdiverse rainforests were niche specific, and I published a pioneer paper to that effect.

Also presenting at the conference was someone unfamiliar to me from the University of Iowa, Steven Hubbell. His paper gave me a shock! His approach and conclusion were dramatically different from my own. He had established one large tree-demography plot that covered 124 acres (50 hectares) on a relatively uniform and gentle slope on Barro Colorado Island, a research island in the Panama Canal, administered by the Smithsonian Tropical Research Institute. Steve had censused, tagged, mapped, and identified all trees larger than 0.4 inches (1 centimeter) in diameter, numbering over three hundred thousand trees-a staggering figure. From this, he had convincingly shown that the spatial distributions of the species were consistent solely with the constraints of limited seed dispersal from parent trees. He concluded that the species were ecologically complementary with one another and were therefore consistent with the geographical expectations of the theory of island biogeography after all.

Following his session, I was in a state of shock. How then, if at all, could the hundreds of tree species sharing a common habitat distrib-



Stuart Davies is now the director of the Forest Global Earth Observatory (ForestGEO). He holds the Frank Levinson Chair in Global Forest Science and is a senior staff scientist at the Smithsonian Tropical Research Institute.

ute themselves independent of any variation in their physical habitat? I introduced myself and suggested we retire to a neighboring pub to hammer out our differences over a pint or two. We realized that the disagreement likely arose from our different sampling methods: my small plots were distributed across variable landscapes on a regional scale while his single large plot represented a uniform habitat. My plots were too small to detect local patterns, nor had I mapped my trees, while his plot may have been too small to detect habitat-related floristic change in relation to topography, nor had he sampled soils. We agreed that the way forward was to replicate his large plot on the other side of the world. I gained the support of my friend Salleh Mohd Nor, the director of the Malaysian Forest Research Institute, to establish a 124-acre (50 hectare) plot on the gentle topography of Pasoh Forest Reserve. Then, Steve and I successfully persuaded the National Science Foundation to fund it. We would use identical census protocols at both sites and recensus each every five years. The aim was to resolve the central, as yet not fully resolved question: To what extent are rainforest tree species niche specific and to what extent are they spatially restricted by their limited seed dispersal?

I was soon in luck again: the United States ambassador in Thailand, John Gunther Dean, was a resource economist, and he recommended that the State Department should host a regional conference in East Asia on research priorities for the sustainable development of natural resources. The State Department was looking for someone to orchestrate it. I jumped at the opportunity. With support from the National Science Foundation and Agency of International Development, I then toured the region seeking advice from friends and colleagues. It was not difficult to gain consensus for the concept of a regional network of representative forest community samples. The sites would follow Steve's protocol, varying in area such that each captured at least one hundred individuals of half the species represented.

Thus, the Center for Tropical Forest Science (CTFS) was born—an informal collaboration of national researchers and their institutions. This became part of the Smithsonian Tropical Research Institute but was managed from the Arnold Arboretum until my retirement in 2000. CTFS has since expanded to become a component of the Smithsonian's new Forest Global Earth Observatory (ForestGEO). This expansion aims to build international capacity in forest science, monitoring the effects of climate change on natural terrestrial ecosystems. The program is now directed by Stuart Davies, who, as one of my Harvard graduate students, completed elegant field observations and experiments on habitat differentiation within a species-diverse genus of pioneer trees, Macaranga, a member of the spurge family (Euphorbiaceae). Crucially, Stuart had already gained the friendship of our regional partners. Although still best represented in East Asia, there are now sixtyseven forest research sites worldwide, including one at Harvard Forest, and more than six million individual trees monitored. More than four hundred published peer-reviewed papers underwrite the massive acceleration in our knowledge of forests.

The CTFS focus on understanding tropical rainforest species diversity continues, but the work has revealed unexpected patterns: Plot species diversity, instead of increasing with habitat favorability, unexpectedly peaks at quite low levels of soil nutrients. This, interestingly, supports a theory advanced by ecologist David Tilman, now at the University of Minnesota, in his Princeton doctoral dissertation. He predicted that the low species diversity of plant communities in habitats that are severely limited by low fertility, drought susceptibility, or shadiness is enhanced once these limiting factors start to relax. As soon as these factors relax past a certain threshold, however, one or a few of the species that grow fastest overtop the rest, suppressing subsequent diversity by competitive shading or by hindering establishment. The pattern shown by our plots confirmed the prediction remarkably, independent of the distance between plots.

But that is not the whole story. We are still left with insufficient explanation as to how so many tree species can co-occur in a single community. Some years later, our postdoctoral researcher Koichi Kamiya used molecular genetic analysis of seedlings beneath a grove of four distinct but related *Shorea* species and found that although many were hybrids, very few of the reproductively mature trees were of hybrid origin. This provided clinching evidence that selective mortality results in survival only of those individuals that retain the parental genome and reoccupy the parental, as yet undefined, niche.

Competitive selection also leads to differentiation of flowering times, stature, and response to light among sister species, but these explanations are surely insufficient explanations for the co-occurrence of this incredible biodiversity. Joseph Connell, at the University of California, and Dan Janzen, at the University of Pennsylvania, independently proposed that high diversity could be maintained if each species were to attract a single seed predator, such that seed mortality (causing fewer juveniles near parent trunks) would lead to space available for the establishment of others. But no vertebrate seed predators are so specialized. Czech entomologist Vojtech Novotny has convincingly shown, through studies in New Guinea, that herbivorous insects attack at a generic rather than species level. Instead, researchers, notably Yale professor Liza Comita and her students at the Barro Colorado Island plot, have discovered that the prevalent mortality of established seedlings in hyperdiverse rainforest tree communities is mediated by host-specific pathogenic microorganisms, especially fungi and viruses. If mature populations of particular tree species are less dense, the seedlings are less chemically defended. These less-common species include

trees whose seeds and pollen are the most widely dispersed, including species like the wild progenitors of cultivated mangoes (*Mangifera*), rambutans (*Nephelium*), and durians (*Durio*), which produce few fleshy fruits that are sought by mammals and large birds.

Now, with hundreds of findings resulting from the CTFS coordination and research continuing to expand, we can conclude that niche specificity does indeed govern floristic structure within and between tree species in hyperdiverse plant communities such as rainforests, except at very local levels where the pull of limited seed dispersal is influential. As such, the pub dispute with Steven Hubbell, back in 1982, can be resolved: ecological niches occupied by particular species become increasingly specialized over time thanks to competitive interactions, so MacArthur and Wilson's theory of island biogeography can generally be applied to rainforest tree biodiversity at the local scale (a habitat island), but the theory rarely applies more broadly, because climate or geological changes ensue before an equilibrium can be reached in the number of large, long-lived plant species that might eventually occupy a nationsized island.

When I first began my research career in Borneo, in 1957, the limitless lofty forests, the unforgettable aromas, and the bird-and-cicada orchestra echoing through the cathedral-like subcanopy were nothing short of glorious. Things are now so very different. The two British colonies, Sabah and Sarawak, united as states within independent Malaysia at an ominous time. Peninsular Malaysia had gained independence in 1957, at the moment when the African oil palm (*Elaeis guineensis*) was beginning to be a serious commercial competitor to the Brazilian rubber tree (*Hevea brasiliensis*), causing increased demand for new agricultural land. Agronomists in Peninsular Malaysia recommended that all soils that supported mixed dipterocarp forest were suitable for oil palm cultivation. Legal constraints on timber exports were relaxed. The international trade peaked, with oversupply depressing prices. Sustainable forest management languished. Now, Pasoh contains the only inland mixed dipterocarp forest remaining unlogged in Peninsular Malaysia outside the parks.

In Borneo, the same fate awaited mixed dipterocarp forests ten years later. With dominance of demand from Japan, and later China, a local wood-based industry, which had benefitted from government investment in research such as mine, went into decline. Brunei, prospering from its oil, has alone retained aboriginal forest over two thirds of its modest land area, timber harvesting being allowed only for the home market. My initial campsite in Brunei, back in 1957, at Kuala Belalong, now hosts a university forest research and training camp, while our plots in the Andulau hills, closer to the coast, are now encompassed within a research preserve and an adjacent forest service research station.

In Sabah, thanks in part to political gains among the inland communities, a successful expansion of an ecotourism industry, and an outstanding and farsighted director of forests, Datuk Sam Mannan, large tracts have been conserved and riparian fringes protected. But Sabah was far from immune to events that happened in Peninsular Malaysia and those that followed in Sarawak, where politicians saw timber licenses as a ready bribe to induce candidates to change sides. In Sarawak, politicians and their families became the new rentier elite, with the power to delegate timber licenses, awarded over periods that often corresponded with elections rather than felling cycles of fifty years or longer. Licenses were, in turn, delegated to companies of industrious and enterprising overseas Chinese, who have used their profits to expand their operations as far as New Guinea and South America. Young Dayaks hazarded their lives as saw operators at one hundred dollars a day, too often with tragic consequences. Now, other than in the parks, little of the original rainforest remains in Sarawak.

On climbing the basalt peak of Bukit Mersing, in central Sarawak, I recall looking down in wonder on the lavender cascades of the rare strangler *Wightia borneensis* in flower. But, years later, a silviculturist apologetically confessed to me that this magnificent park, which I had proposed given its rich diversity of rare

Eusideroxylon zwageri is a rare tree in the laurel family (Lauraceae), which is listed as vulnerable on the International Union for Conservation of Nature's Red List of Threatened Species.





Oil palm (Elaeis guineensis) cultivation has created a massive conservation threat for mixed dipterocarp forests in Southeast Asia.

and endemic species, had "inadvertently" been licensed for logging. Our permanent plots there were trashed, and those in coastal Nyabau forest were cleared for an oilfield service depot. Of all our thirteen plot sites in Sarawak, only three remain unfelled. Although smallholder plantations have increased, the relegation of formerly reserved forests to commercial interests has sanctioned a massive transfer of wealth from the rural poor to the new urban rich. Sarawak's national parks and strict preserves, unique among rainforest conservation areas, were selected and demarcated on botanical and ecological criteria rather than mammalian fauna. In the absence of any policy for retaining the animal migration paths, riparian forests between all but two of Sarawak's national parks have been destroyed, and most of the parks are consequently too small to sustain all but populations of the smallest vertebrates.

In the summer of 2019, while writing this essay, I received the following from an old

Sarawakian friend, Paul Chai, who succeeded me as forest botanist in 1966 and, like me, is long retired: "No good news on forestry. Sarawak is experiencing annual haze due to burning in Kalimantan and here, and Miri is worse.... I am worried that other national parks may soon be at risk. Enforcement is poor and relies on drones and helicopter." This tragedy has resulted from the meteoric rise of China in the international timber trade—a country which has evolved exemplary conservation policies for its own natural resources but which imposes no rules on its overseas commercial interests, including imports of timber, and animals and plants of value for traditional medicine. Yet to whom, ultimately, should the accusing finger be pointed? China now exports more than half the world's furniture, and most of that production is purchased in the West.

So, I wonder, have I been wasting my time? Laboring in this depressing environment, though, are two outstanding young Iban



A mixed dipterocarp forest has been cleared and terraced for oil palm cultivation.

women—Julia anak Sang and Wilhelmina anak Cluny, respectively a field botanist and a wildlife naturalist—doing their best to turn the tide with courage and determination. Julia works in the Sarawak Timber Corporation and has a team of forest botany technicians who search the degraded forests for surviving tree flora. She is publishing Red List data for the International Union for Conservation of Nature and is mapping and documenting current species conservation status within and outside the protected areas. Wilhelmina is a conservation officer in the Sarawak Forest Department who has focused on vertebrate conservation. She has worked on enhancing local community involvement in protected area conservation, especially Kayan Mentarang National Park, a large park that spans the border between Sarawak and the Indonesian territory of Kalimantan.

Conservation and forestry are not fundamentally incompatible, but given the current status of forest degradation in this region, how long would it take to restore a sustainable felling cycle? Probably fifty to one hundred years. How long to restore the original forest carbon mass? At least one hundred. And species diversity? Even if there is no local extinction, probably at least a millennium. I'm hopeful, at least, that our research and the continued work of CTFS and ForestGEO can provide the information necessary for restoring, in the future, the unimaginable diversity of these rainforests.

Reference

The map for this article was created using Esri, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community.

Peter Ashton is Harvard University Bullard Professor Emeritus and was director of the Arnold Arboretum from 1978 to 1987. Among many career honors, his research on tropical forests was recognized with the prestigious Japan Prize in 2007. He and his wife, Mary, live in Chiswick, London. This *Arnoldia* article is the third and final in a series about Ashton's research career.

E.S. Rogers and the Origins of American Grape Breeding

J. Stephen Casscles

n the mid-nineteenth century, eastern Massachusetts was a hub for American horticul-Ltural talent, including writers and nursery owners. In the case of fruit breeders like Edward Staniford Rogers, even work conducted at a relatively small scale had the potential to spread nationally, shaping breeding efforts into the present. Rogers focused on grapes, and he did his work in his half-acre backyard at 376 Essex Street, in Salem, Massachusetts. Rogers came from a prosperous mercantile and shipping family, and in 1826, the year Rogers was born, Essex Street was one of Salem's wealthiest residential neighborhoods. The street ran into the city's center, near the wharves of Salem Harbor, then one of the busiest ports on the Atlantic seaboard.

Rogers began his breeding work in 1851, when he was still a young man. While shy with most people-some would even say reclusive-he could talk endlessly about his new hybrid grape creations and did so regularly with local and nationally renowned horticulturists. In the process, he became a leading American grape breeder, focusing on hybridizing the common European grapevine (Vitis vinifera) with the hardier and more disease-resistant American fox grape (V. labrusca). Ulysses Prentiss Hedrick, the chief horticulturist of the New York State Agricultural Experiment Station, extensively wrote about Rogers's work and noted, in 1908, that when Rogers introduced his grapes to the public in the late 1860s, "enthusiasm and speculation ran riot." Another breeder, James H. Ricketts of Newburgh, New York, had released successful varieties around the same time, and it was, according to Hedrick, a "golden era" for American grapes. "Possibly at no other period has interest in grape-growing been so keen as during the decade succeeding the introduction of these hybrids," he wrote.

A Horticultural Renaissance

As a grape grower and winemaker, I came to appreciate the landmark hybridization work of Rogers while researching and acquiring cool-climate grape hybrids that were developed in France between 1860 and 1940—primarily crosses between Vitis vinifera and American species like V. labrusca, V. aestivalis, V. riparia, and V. rupestris. I became attuned to these French-American grape hybrids starting in 1974, first by working at Benmarl Vineyards, in Marlboro, New York, and subsequently at the Hudson-Chatham Winery in Ghent, New York, where I encountered red grapes like 'Baco Noir' and 'Chelois' and white grapes like 'Seyval Blanc' and 'Vidal', along with more than a dozen others.

My interest then led me to Rogers and other East Coast hybridizers, including a significant number based in the Hudson Valley. I evaluated the Rogers varieties to see if they could be grown in a more ecologically sustainable manner than grape varieties that are conventionally grown today, and I wanted to learn more about the flavor profiles of these forgotten old varieties. For over fifteen years, I have grown twelve of these Rogers hybrids very successfully on my farm, Cedar Cliff, in Athens, New York, for wine production. It is my hope to reintroduce some of the Rogers grapes to commercial growers and wineries so that they can be made more readily available to the public.

In the process of researching heirloom grape varieties, I discovered that, between 1840 and 1890, eastern Massachusetts and the Mid-Hudson Valley were two of three centers of grape breeding. Breeders were also busy near St. Louis, Missouri. In Massachusetts, the breeders were generally wealthy New England Brahmins, like Rogers, whose families made fortunes either as merchants or in mercantile shipping.

Edward Staniford Rogers began hybridizing American and European grapes in 1851, launching an era of "enthusiasm and speculation" for American grape growers. All images, unless indicated, are from *The Grapes of New York* by Ulysses Prentiss Hedrick.





The American fox grape (*Vitis labrusca*, left) is well-known for being a parent of the spontaneous hybrid 'Concord' (right), which is often used for jellies and juices.

These genteel farmers engaged in horticulture for intellectual stimulation and social comradery. Nursery owner Charles Mason Hovey facilitated communication between nearby breeders and regularly corresponded with the national fruit-breeding community either in person or through the many plant catalogues, pamphlets, and horticultural books that he wrote. In addition, Hovey helped to direct, along with Marshall Pinckney Wilder, the nationally recognized Massachusetts Horticultural Society and the American Pomological Society. Local agricultural and horticultural societies were also actively evaluating new horticultural varieties in most eastern Massachusetts counties.

Several forces compelled these Massachusetts horticulturists to develop new hybrid fruit. Many desired to create plant material for their suburban and rural homes, emulating the British landed gentry and securing greater social prestige within their community. Others desired to develop fruits that were more productive and disease resistant for profit. An underlying theme was the uniquely New England quasi-religious-social-ethical belief among business, social, and religious leaders that one's religious service could be manifest by service to community. Work had a moral component, and the highest calling was to be productive; unlike the trading of goods, engaging in agriculture and manufacturing was a divine calling.

Further, by 1800, the region's already thin agricultural soils were becoming very depleted due to more than a century of extensive but unwise cultivation techniques and practices. Hence, a movement arose to study agriculture, hybridization, and plant sciences, so that local farmers could revitalize their increasingly poor and overcropped soils. The business community supported these agricultural research initiatives so that farmers would remain in Massachusetts and continue to be their loyal



Rogers made careful crosses between the fox grape and the European wine grape, *Vitis vinifera* (left). He used a common variety known as 'Black Hamburg' (right).

customers, instead of being forced to move farther west in search of more fertile soils. The business community's support was evidenced by the founding of the Massachusetts Society for Promoting Agriculture in 1792. Its membership was clearly mercantile in composition, including most of eastern Massachusetts's prominent families, along with attorneys and a few physicians and clergy, most of whom were Harvard College alumni.

Hybrid Crosses

Even within this vibrant horticultural milieu, Rogers was unique. According to Thomas Volney Munson, a central figure among the next generation of American grape breeders, Rogers was responsible for taking "the first intelligent step" towards developing "thorobred" American grape varieties. Unlike the classic 'Concord', which was selected by Ephraim W. Bull from a spontaneous cross between *Vitis* *labrusca* and *V. vinifera* (the results of natural insect pollination) in Concord, Massachusetts, in the 1840s, Rogers was intent on carefully making and documenting his crosses. In his own words, Rogers said, "When I commenced experimenting I had no knowledge of any one who had raised grapes by this process, though I had heard of flowers, pears, &c., and I had attempted crosses of pears. Reading articles in the London *Horticulturalist*, it occurred to me that I could get a new grape by this process; combining the qualities needed for open culture, it would be more valuable than any other fruit."

Rogers was drawn to the quiet and contemplative life of horticulture, and once his father died in 1858, he very quickly exited the family shipping business and concentrated on his horticultural pursuits and real estate investments in Rockport, Massachusetts. He wanted to create new grape varieties that incorporated the more sophisticated and subtle flavors of European *Vitis vinifera* varieties (like the table grapes we buy today in the supermarket) with the hardiness and reliable productivity of native American grape varieties, ripening early, before the first fall frost. Successful varieties also needed to possess ample fungal disease resistance and simultaneously be productive enough as commercial table grapes, with big berries, big clusters, sufficient sweetness, and skin that adhered to the flesh of the berry.

In the summer of 1851, Rogers made crosses using a seed parent, Vitis labrusca 'Carter' (a wild-type variety also known as 'Mammoth Globe'), and the pollen of V. vinifera 'Black Hamburg' and 'White Chasselas'. 'Carter' was used as the seed parent because this self-sterile variety was large fruited, hardy in the field, and one of the earliest ripening local selections that he could find. The pollen of 'Black Hamburg' and 'White Chasselas' was chosen because they were two of the hardiest European varieties and were the most commonly available in Massachusetts. The pollen was obtained from vines growing in a nearby unheated glass greenhouse. The exact provenance is unrecorded, but the pollen could have come from someone like John Fisk Allen, who lived about two blocks from Rogers, or George Haskell, in nearby Ipswich. Both men were highly interested in grape cultivation.

The 'Carter' blossoms were emasculated and fertilized with Vitis vinifera pollen and small cotton bags were placed over the 'Carter' female flowers. Rogers also placed clusters of V. vinifera blossoms in the bags. From this cross-pollination, he secured about 150 seeds. These seeds were then planted in his backyard garden that fall. The following spring, many of these seeds germinated, but cut worms and other accidents reduced the number of vines to forty-five. These forty-five vines grew upward on poles for three years. Due to overcrowding, Rogers transplanted twenty-five of the plants to other parts of the garden to give them enough room to grow. The untransplanted vines started to bear fruit in 1856, and the transplanted varieties fruited a few years later. In observing the garden, Marshall Pinckney Wilder, of the American Pomological Society, said, "How much can be done with little is illustrated by the fact that all [of his grapes] ... were produced by a lame man in a half-acre city lot 150 years in cultivation." Further, he noted that the lot was "a cold matted soil filled with old apple and pear trees, currant bushes, flax and everything mingled in together."

Rogers believed his grape creations to be a success, noting the intermixture of traits between the species. "The vines are even more vigorous than the parents," he wrote, "and more exempt from diseases, and more hardy than most outdoor varieties." The seedlings were numbered one to forty-five. In 1858 and 1859, Rogers sent cuttings of these numbered varieties to growers and horticulturists for further testing. He disseminated these varieties due to the small size of his backyard garden and because the common practice then, as it is now, was to share plant material with colleagues to get comments on the growing attributes, strengths, and weaknesses of such plants in a wide range of climates and soil types.

Through his painstaking work, Rogers created over twenty major grape hybrids. The resultant grapes were first officially introduced to the public in 1867. In 1869, Rogers named thirteen of his varieties after local Massachusetts places and people ('Agawam', 'Massasoit', 'Salem', 'Essex', and 'Merrimac'), as well as for horticulturists ('Barry', 'Lindley', 'Gaertner', and 'Wilder') and the German writer Johann Wolfgang von Goethe ('Goethe'). These were promoted through the Catalogue of Fruits by the American Pomological Society, an organization that was based in Boston. From there, the Rogers hybrids steadily gained interest and notoriety across the United States and Canada.

The Rogers Grapes

All Rogers hybrids possess large or very large berries, medium-sized clusters, and grape skin that is either attached or semi-attached to the berry flesh, unlike the "slip-skin" characteristic of the 'Concord'. They grow vigorously, have better fungal disease resistance than their European pollen parents, and are hardy and

American Grape Breeding 35



By 1869, Bushberg Vineyards and Orchards, in Missouri, promoted many of the Rogers grape varieties in their *Illustrated Descriptive Catalogue of Grape Vines, Small Fruits, and Seed Potatoes.* Of 'Goethe', the catalogue advertised, "At the fall meeting of the Mississippi Valley Grape Growers' Association, September 9, 1868, we exhibited for the first time a few branches of the vine, each with several perfect clusters, which were much admired, and would have probably astonished even its originator, could he have seen them."

productive. I like the growing characteristics of the twelve Rogers hybrids that I cultivate in the Mid-Hudson Valley, and the resultant fruit is flavorful and makes wonderful wines that have an attractive combination of soft flavors of Muscat grapes and *Vitis labrusca*.

These characteristics made the Rogers hybrids very popular when first introduced to America and Canada in 1867. They were initially quite sought after by growers, talked about at horticultural and agricultural society meetings, and widely evaluated. In 1895, the nationally recognized Bushberg Vineyards catalogue, which set the standard for fruit catalogues and pomological literature in North America, extensively covered the Rogers hybrids with accompanying illustrations of many of them. The Bushberg catalogue stated that these Rogers varieties were "very productive," "beautiful," and "valuable" selections that were "handsome in appearance" and of "fine quality" for the table and for wine. Other definitive North American nursery catalogues of the latter nineteenth century, including Hovey's The Magazine of Horticulture, prominently featured and illustrated the Rogers hybrids, as did agricultural magazines like The Gardner's Monthly and Horticulturist, The Rural New Yorker, and The Country Gentleman.

Among Rogers's selections, 'Agawam' is one of his best. In 1908, Hedrick reported that 'Agawam' was the most widely grown of the Rogers hybrids, noting that it was sold by practically all nurseries in the United States east of the Rocky Mountains. It is the only completely self-fertile of the Rogers varieties. The color is a dark purplish-red with a lilac bloom. The wines are aromatic with rich fruit flavors of Muscat grapes and hints of fresh grapes, guava, and tropical fruits from Vitis labrusca, along with an herbal finish. The body is substantial and viscous for a white wine, and it can either stand alone or be used in blends with other white wines. Tasting something like this is to taste the nineteenth-century innovation of Rogers and his contemporary fruit breeders in Massachusetts, the Mid-Hudson Valley, and the St. Louis area.

The Rogers Hybrids Live On

A combination of factors led to dwindling name recognition for the Rogers grapes. Hedrick stated that the period between 1853 (the date 'Concord' was first introduced) and 1880 could be "singled out as the period in which viticulture made its great growth in eastern America." After 1880, however, California started to compete in earnest with eastern vineyards, and grape prices fell significantly in eastern metropolitan markets, given the vast influx of inexpensive California grapes. This competition, combined with higher incidence of fungal diseases and insect damage in eastern vineyards, which were planted too closely to one another, severely reduced overall production in the east. With a corresponding reduction of grape acreage, varieties like 'Concord', 'Niagara', and 'Delaware' expanded their dominance, while the Rogers hybrids, which, save for 'Agawam', were mostly self-infertile, declined relatively and absolutely in acreage. In addition, the enactment of Prohibition in 1920 further reduced their demand for wine production, which was their primary use.

Yet the Rogers hybrids live on in the twentyfirst century. In the Rogers era, privately organized horticultural and agricultural societies, such as the Massachusetts Horticultural Society, sponsored the bulk of the public discussion about plant evaluation. However, with the Congressional enactment of the Morrill Act of 1862 (establishing agricultural land-grant colleges) and the Hatch Act of 1887 (establishing agricultural experiment stations), this horticultural domain shifted increasingly to government-financed programs. With this shift, many of the Rogers grapes were incorporated into the most advanced American cool-climate, wine-grape breeding programs of the twentieth century. For example, at Cornell University, the Rogers hybrid 'Herbert' was used to breed the hybrids 'Sheridan', in 1921, and 'Buffalo', in 1938. These, in turn, lead to the development of twenty-first-century introductions like 'Geneva Red', 'Corot Noir', and 'Noiret'. Elmer Swenson of Wisconsin, whose private breeding program was subsequently absorbed into research at the University of Minnesota, used



The author considers 'Agawam' to be the finest Rogers variety for modern winemaking.



While the fame of the Rogers grapes waned in the early twentieth century, 'Goethe' (left) has found unexpected popularity in Brazil. Also shown: 'Lindley'.

the Rogers variety 'Wilder' as a great grandparent to create 'Marquette'. The varieties 'Marquette' and 'Noiret' are now finding their place in today's North American cool-climate wine industry. In addition, Rogers varieties were used in the breeding programs at agricultural experiment stations in Missouri and South Dakota. Thomas Volney Munson, the pioneer American grape breeder who privately bred many scores of high-quality hardy and disease-resistant grape varieties for the central and southern United Sates, relied heavily on Rogers hybrids for his extensive breeding program.

The Rogers varieties do not simply persist as the basis for subsequent breeding efforts. The variety 'Goethe' is the foundation of one niche segment of the Brazilian wine industry in the Urussanga region of the state of Santa Catarina. In Brazil, 'Goethe' is made mostly into sparkling wines with vineyards that cover over one hundred acres. While 'Goethe' is traditionally a pinkred variety, a natural mutation, first observed in a Brazilian vineyard the 1950s, has produced a white clone, now known as 'Goethe Primo'. This new variety makes still and sparkling wines that are very *Vitis vinifera*-like in their flavor profile and acid balance but with pleasant, soft aromatics from *V. labrusca*. In this region, over twenty thousand gallons of 'Goethe' wine are produced, with the remainder sold as table grapes.

Today, commercial and hobbyist growers, foodies, farm-to-table advocates, private grape breeders, and university breeding and agricultural research programs are all looking for the "next best" fruit variety that is flavorful and productive and which can be grown in a more environmentally sustainable manner. The Rogers hybrids, along with other heirlooms bred in New England and in the Hudson Valley, fit that bill. Rogers's work demonstrates that sometimes the search for the "next best" may involve looking back.

References

- Bush & Son & Meissner, Bushberg Vineyards. 1895. Illustrated descriptive catalogue of American grape vines (4th ed.). St. Louis: R.P. Studley and Co.
- Casseles, J.S. 2015. Grapes of the Hudson Valley and other cool climate regions of the United States and Canada. Coxsackie, NY: Flint Mine Press.
- Cedar Cliff Nursery. 2013–2019. Cedar Cliff Nursery: Grape vines for grape growers and field & cellar notes. Catskill, NY: Casscles, J.S.
- Downing, A. J., and Downing, C. 1869. *The fruits and fruit trees of America* (2nd ed.). New York: John Wiley & Sons.
- Hedrick, U. P. 1908. *The grapes of New York* (Annual report of the State of New York, Department of Agriculture; no. 15, v. 3, pt. 2). Albany, NY: J.B. Lyon Company.
- Hedrick, U.P. 1933. A history of agriculture in the State of New York (The New York State Agricultural Society). Albany, NY: J.B. Lyon Company.
- Hedrick, U.P. 1950. A history of horticulture in America to 1860. New York: Oxford University Press.
- Hedrick, U.P. 1919. *Manual of American grape-growing*. New York: The Macmillan Company.
- Hovey, C. M. The magazine of horticulture, botany, and all useful discoveries and improvements in rural affairs. Boston: Hovey and Co.
- Hutchinson, B.J. 1980. A taste for horticulture. *Arnoldia*, 40(1): 31–48.
- McLeRoy, S., and Renfro, R.E. 2008. *Grape man of Texas: Thomas Volney Munson and the origins of American viticulture.* San Francisco: The Wine Appreciation Guild.

- Morton, L. T. 1985. Winegrowing in eastern America: An illustrated guide to viniculture east of the Rockies. Ithaca, NY: Cornell University Press.
- Munson, T.V. 1909. Foundations of American grape culture. New York: Orange Judd Company.
- Parker, S. J. 1865. Improvement of native grapes by seedlings and hybridization. In *Report of the Commissioner of Agriculture for the Year 1864* (pp. 122–136). Washington, DC: Government Printing Office.
- Rogers Family Papers, Peabody Essex Museum (MSS 87). Phillips Library at the Peabody Essex Museum, Salem, Massachusetts.
- Schofield, E. A. 1988. "He sowed; others reaped": Ephraim Wales Bull and the origins of the 'Concord' grape. Arnoldia, 48(4): 4–15.
- Thorton, T. P. 1989. *Cultivating gentlemen: The meaning* of country life among the Boston elite, 1785– 1860. New Haven, CT: Yale University Press.
- Wagner, P.M. 1969. American wines and wine-making. New York: Alfred A. Knopf.

J. Stephen Casscles comes from a fruit-growing family rooted in the Hudson Valley since the 1870s. In 1990, he established a four-acre vineyard, Cedar Cliff, in Athens, New York, where he has concentrated on identifying, growing, evaluating, and propagating heirloom grape varieties that were first developed in New York in the mid-nineteenth century. He has been the winemaker at Hudson-Chatham Winery, in Ghent, New York, since 2008. In 2015, he published a book on historic grape cultivation titled *Grapes of the Hudson Valley and Other Cool Climate Regions of the United States and Canada* with Flint Mine Press.

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A Teacher's Favorite: Gleditsia aquatica

Ana Maria Caballero McGuire

E veryone knows that teachers should not have favorites, but I do. My favorite has muddy feet, a thorny disposition, and reddish-brown, almond-shaped eyes. Oh, and he's also a southerner. *Gleditisa aquatica* (accession 201-93*B), also known as the water or swamp locust, is a North American native, closely related to the more familiar honey locust (*G. tricanthos*). You will find the species growing along riverbanks and marshes in its natural range, stretching from South Carolina to central Florida, across Louisiana to eastern Texas, and up the Mississippi River valley to southern Illinois and Indiana. My Arboretum favorite was wild collected in southeastern Missouri.

When I introduce children to this tree at the Arboretum, I often start with, "Who here is brave, really brave? I want to show you a dangerous plant." That usually elicits excitement and a loud chorus of "Me!" I bring them to Rehder Pond, where they stand looking very closely at the tree behind me. It can take a minute before they understand what they are looking at: a profusion of three- to five-inch-long reddish-brown thorns growing both on the lower parts of the trunk and out along the branches. I often clip a sample and model how to use a one-finger touch along the edge of the thorn to compare its smoothness with the sharp prickly point. It doesn't take long before many children begin to touch the thorns and even ask if they can hold it. They remind me of times when my brothers and I would beg our parents to give us their plastic sword cocktail picks, and we would sword fight in the restaurant while waiting for our meals!

Once the children are comfortable with the thorns, we begin a conversation around function. Why would this tree have such thorns? Students quickly identify defense as the main function but then are stumped when asked what the tree is defending itself from. The most common answer is people and predators like foxes, lions, and sharks. It takes some pretend modeling of large herbivores eating before children understand how this tree, having large, thick, and sharp thorns growing at the base of each bipinnately compound leaf might deter large mammals—whether living (deer) or extinct (mastodon)—from eating the leaves.

One season I noticed that an American robin (*Turdus migratorius*) had built a nest on a low branch. In the nest were three young chicks, and the momma was busy flying back and forth, attending to their needs. I used this opportunity to continue the thorn discussion by posing a new question: "Is that robin smart for building a nest in this thorny tree?" The group was evenly split between yes and no. Each child had to state their opinion and provide a reason for their answer. In this way, I encourage children to take what they know and what they observe firsthand to form a more complete understanding of how nature works. They also learn to debate by listening to differing views.

Aside from thorns, *G. aquatica* also produces curious eye-shaped seedpods, about 1.5-inches long and flat. Before the seedpod dries out and turns a rich caramel brown color, children can raise the fruit to the sky and see through the papery thin walls to the singular round seed in the middle. Two of these seedpods placed over my eyes elicits cries of "Owl eyes!" This fruit is unique among all *Gleditsia* species because it does not contain a sticky, honey-like pulp surrounding the seeds, and it usually has one seed, rather than ten or more like the honey locust. This difference has led some botanists to suggest that *G. aquatica* evolved to disperse its seeds via water, instead of animal digestion.

Finally, how can I resist a quick math lesson when observing the leaves? The compound leaves measure up to thirty inches long, and the small leaflets occur in six to fourteen pairs on a leaf. They are perfect for a lesson about odd and even and help facilitate counting by twos. Later, children line up in pairs, just like their leaf, and count by twos as they slowly walk back to their bus, heads full of wonder and a pocket or two hiding large owl eyes.

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