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Front and back cover: Andrew Robeson prepared maps for Charles Sprague Sargent's *Report on the Forests of North America (Exclusive of Mexico),* published in 1884. This map shows "relative average density of existing forests" across the country, which was calculated in the number of cords of lumber that could be harvested per acre. Regions marked with Roman numeral I were estimated to yield less than one cord per acre, while those marked with VII (the highest in the eastern United States) were estimated at fifty to one hundred cords. Map from Arnold Arboretum Archives.

Inside front cover: Railroads allowed Ernest Henry Wilson rapid access to collecting locations in Taiwan. On March 12, 1918, he photographed a man standing on railroad tracks with a large specimen of *Vitex quinata* (a member of Verbenaceae, then known as *V. heterophylla*) reaching overhead. Notice the epiphyte-laden branches. Photo from Arnold Arboretum Archives.

Inside back cover: The Sax pine (*Pinus monticola* × *parviflora* var. *himekomatsu*) retains the blue foliage of the Japanese white pine, one of the hybrid parents. Cones were observed on accession 266-46*F. Photo by Jonathan Damery.

GROSSMAN, J. J. 2019. THE HYBRID MYSTIQUE. *ARNOLDIA*, 76(3): 2–13

The Hybrid Mystique

Jake J. Grossman

Hybrids, the results of successful breeding between two parents of different species, occur frequently in nature, yet are perhaps most familiar to us when they result from human intervention. We encounter in our intentionally cultivated hybrids the utility of the mule, the stateliness of the London plane tree, and the sensuous smells and tastes of myriad vegetables and fruits, including broccolini and the tangelo. These remarkable examples are of our own making, but hybridization between closely related species is perhaps the norm rather than the exception in nature. Though hybrid offspring are sometimes sterile and can be visually distinct from their parents (like mules), they are just as likely to be fertile and to pass unnoticed by us. These cryptic hybrids, diagnosable only through genetic testing, breed with each other or with individuals of their parent species (in a process called backcrossing), giving rise to new hybrid progeny. Over generations, such interbreeding consolidates novel hybrid traits, sometimes leading to the formation of new species. Because what counts as a species is, after all, merely conventional, it could be said that we humans, the descendants of interbreeding between Neanderthals and early *Homo sapiens,* are just as much hybrids as the most luscious of tangelos. Perhaps foremost among the natural world's "hopeful monsters"—a term that geneticist Richard Goldschmidt coined in 1940 for evolutionary transformations that occur through rare but large-scale mutation—hybrids often captivate and delight human observers.[1]

Yet hybridization does not always precipitate the formation of a new species. In natural populations, hybrids are frequently formed, only to be subsumed, through backcrossing, into their parental stock. This process—called introgression—results in the enrichment of the gene pool of the predominant species with genetic material from close relatives. So, in the case of oaks—described as particularly problematic for the biological species concept due to their wanton tendency to hybridize (Burger, 1975)—we might say that there is evidence of red oak (*Quercus rubra*) introgression into a stand of northern pin oaks (*Q. ellipsoidalis*). These pin oaks will still be *pin oaks,* but perhaps with some hidden genetic diversity and leaves or bark that look, well, just a little bit different. The ubiquity of such situations has led biologists to formulate the idea of hybrid complexes or zones: sets of species or populations in which rampant interbreeding has produced a messy gradient of similar organisms, rather than discrete sets. Our cultivated citruses represent one such complex, in which ten progenitor species in southeast Asia and Australia have given rise, through hybridization, to dozens of domesticated taxa (Wu et al., 2018).

And so, when I began my own foray into the world of hybrid aspens (*Populus*), I risked wading into a thicket of biological questions that could have been difficult or impossible to resolve. Fortunately, I was a first-year graduate student, a neophyte far more optimistic than I am now when it comes to tackling a new project. What follows is a story of a journey through which a team of ecologists and evolutionary biologists, myself included, tried to track down the truth about a putative hybrid. To do so, we traveled throughout the Midwest and dug deep into the natural history of the Niobrara River Valley, a relictual ecoregion left behind by the retreat of glaciers at the end of the last Ice Age.

A biotic crossroads: The Niobrara River Valley

Heading into the Nebraska Sandhill region along the state's border with South Dakota, new visitors might be surprised to plunge from cornfields and pastures stretching as far as the eye can see into forested canyons hugging a cool, inviting river. Originating on the eastern edge of Wyoming, the Niobrara River runs from west to east across the northern quarter of Nebraska

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Smith Falls aspens (*Populus* × *smithii*, right) along the Niobrara River, in northern Nebraska, are natural hybrids of two common North American aspen species. It shares habitat with northern species like paper birch (*Betula papyrifera*) and western species like ponderosa pine (*Pinus ponderosa*), both shown at left.

before being subsumed in the Missouri River in the northeastern corner of the state. The canyons found between the river's banks and the surrounding matrix of arid short- and mixed-grass prairie constitute the Niobrara River Valley.

For an eager observer, this valley presents more than just a respite from Nebraska's hot, dry uplands. Rather, as Midwestern botanist Charles Bessey first observed in 1887, the Niobrara River Valley is a "meeting-place for two floras," a unique location in North America in which East and West comingle. Born and raised in Arizona, I had spent about five years living in the Midwest by the time I first visited the valley. When I arrived by car from St. Paul, Minnesota, where I had just begun my doctoral studies as a plant ecologist, it felt like I was seeing old friends again after a long absence. Most noticeably, stands of ponderosa pine (*Pinus ponderosa*), a decidedly western species, greet visitors to the Niobrara. These pines are among over a dozen western vascular plant species whose distributions extend all the way into Nebraska, following the biotic east-west highway formed by the Niobrara River. A second look confirmed that this traffic moved in both directions: bur oaks (*Quercus macrocarpa*) and silver maples (*Acer saccharinum*) made unusual appearances for species that generally cannot be found in great abundance further west than the meeting of the prairies and forests in Minnesota and Iowa. It also became clear that the cooler, north-facing slopes of the valley, in particular, offered suitable habitat for species generally found further north, including cosmopolitan but drought-intolerant paper birch (*Betula papyrifera*). The same pattern—a confluence of biota typical of the montane West, the deciduous forests of the East, and the boreal forests of the North—holds for herbaceous plants, insects, and vertebrates as well (Kaul et al., 1988).

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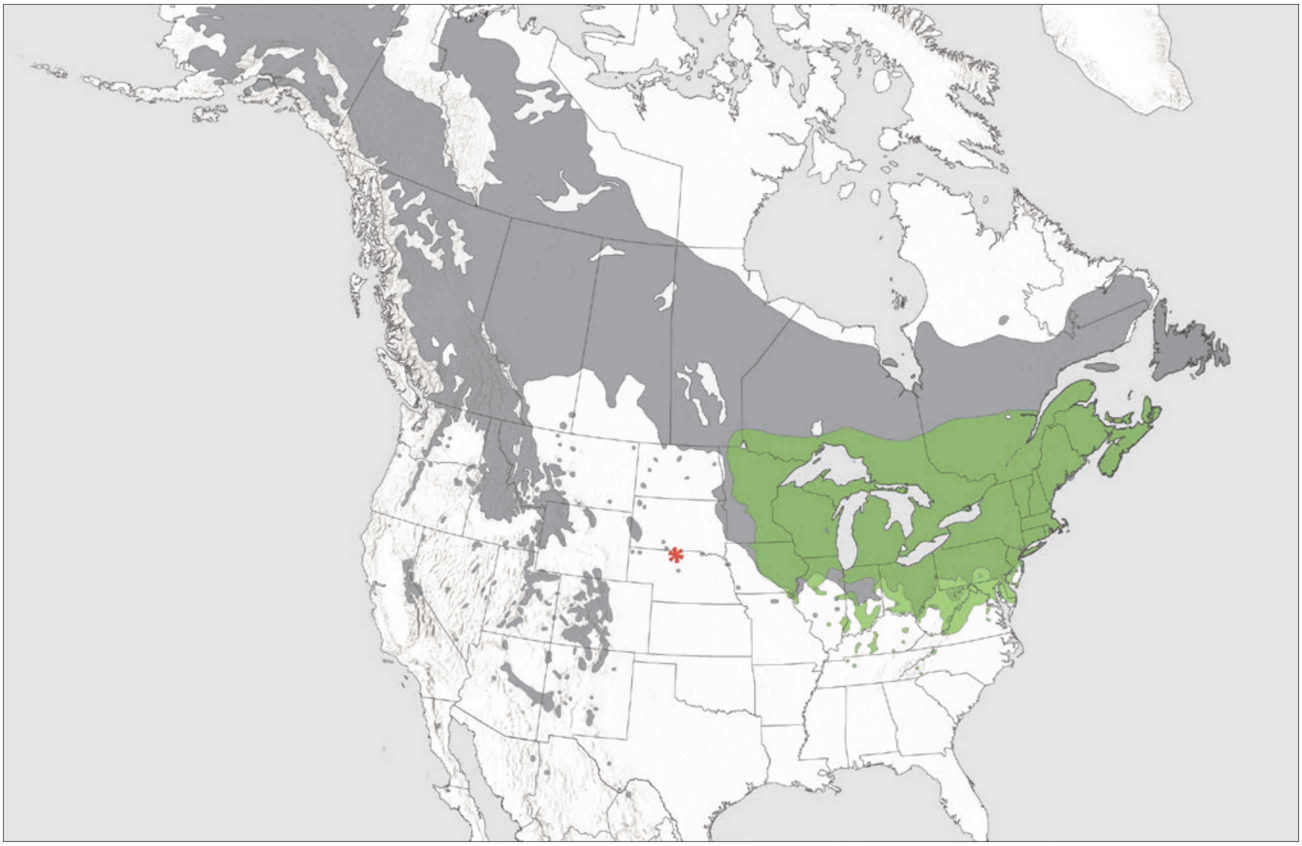
The hills and canyons of the Niobrara River Valley have provided shared habitat for an unusual combination of eastern and western species—plants and animals, alike.

Of aspens, poplars, popples, and cottonwoods

Any exhaustive flora of the Niobrara is bound to mention aspens, meaning species of the genus *Populus.* These trees go by a plethora of common names: aspens, poplars, popples, and cottonwoods—names which do not neatly map on to the current phylogenetic characterization of six sections within the genus (Hamzeh and Dayanandan, 2004). In North America, native species from section *Populus,* and some from *Tacamahaca,* are referred to as "aspens," "poplars," or "popples." These include the ubiquitous quaking aspen (*P. tremuloides*), its close relative bigtooth aspen (*P. grandidentata*), and cold-tolerant basalm poplar (*P. balsamifera*). The species we know as "cottonwoods" are restricted to *Aigieros* and also to *Tacamahaca,* and these include, most famously, eastern cottonwood (*P. deltoides,* one of the largest trees east of the Mississippi), Fremont cottonwood out west (*P. fremontii*), and northwestern black cottonwood (*P. trichocarpa*), the first tree species to have its genome sequenced. Most species in the genus share traits with each other and with other members of the willow family (Salicaceae): they are dioecious, meaning that male and female flowers are borne on separate trees and have simple leaves and relatively short lifespans (often less than one hundred years). Many species have circumboreal distributions; they are generally cold tolerant, but vulnerable to hot and dry conditions.

Aspens writ large have captured the imagination of botanists and the general public alike by virtue of their propensity for perpetuation through vegetative means. Most importantly, this means that a given aspen tree can, regardless of sex, produce new, genetically identical clones of itself. These new stems, often called "suckers," emerge from rhizomes, underground stems that spread in parallel to the



ARNOLD ARBORETUM, US FOREST SERVICE, AND GIS COMMUNITY

The distributions of quaking aspen (*Populus tremuloides*, shown in gray) and bigtooth aspen (*P. grandidentata*, shown in green) present a curious question: how could a hybrid between the two species occur in northern Nebraska, where one parent is exceptionally rare and the other is completely missing?

soil surface. When a rhizome's buds encounter moist, warm conditions, a small shoot heads upward, sprouting leaves and emerging from the soil as though a seed had germinated in that exact spot. But these suckers grow faster than a typical seedling ever could, drawing on resources from their parental plant and bypassing seedling-hood in a mad dash for growth. These clonal offspring can, over time, become separated from their parents through the decay of the rhizome, but they remain genetic clones, such that what often appears to be a stand of aspen trees is, in reality, a single individual, connected, to varying extents, underneath the soil.

The mystery of the Smith Falls aspens

Aspen stands are vanishingly rare, if not altogether absent, in the Great Plains. Quaking aspens (*Populus tremuloides*) are nearly the sole representatives in the region but are restricted to a few tiny islands, usually growing in dense clumps around wetlands. These stands are relics, groups of trees left behind as the global climate warmed over the last ten thousand years. At the end of the Pleistocene Ice Age, aspen species, as with other cold-hardy trees, were probably quite common across this massive inland plain (Wright et al., 1985), but their ranges retracted as the climate became more arid. Stands of quaking aspen in central Canada and in the biotic highways of the Niobrara River Valley provide the only linkages between eastern and western populations for that species. My PhD advisor had secured funding from the National Parks Service—the Niobrara is a National Scenic River—to study one such stand, a rare, and therefore locally famous, collection of aspens centered around Smith Falls State Park, near Valentine, Nebraska. In 2013, we headed out for the first time to see these trees for ourselves.

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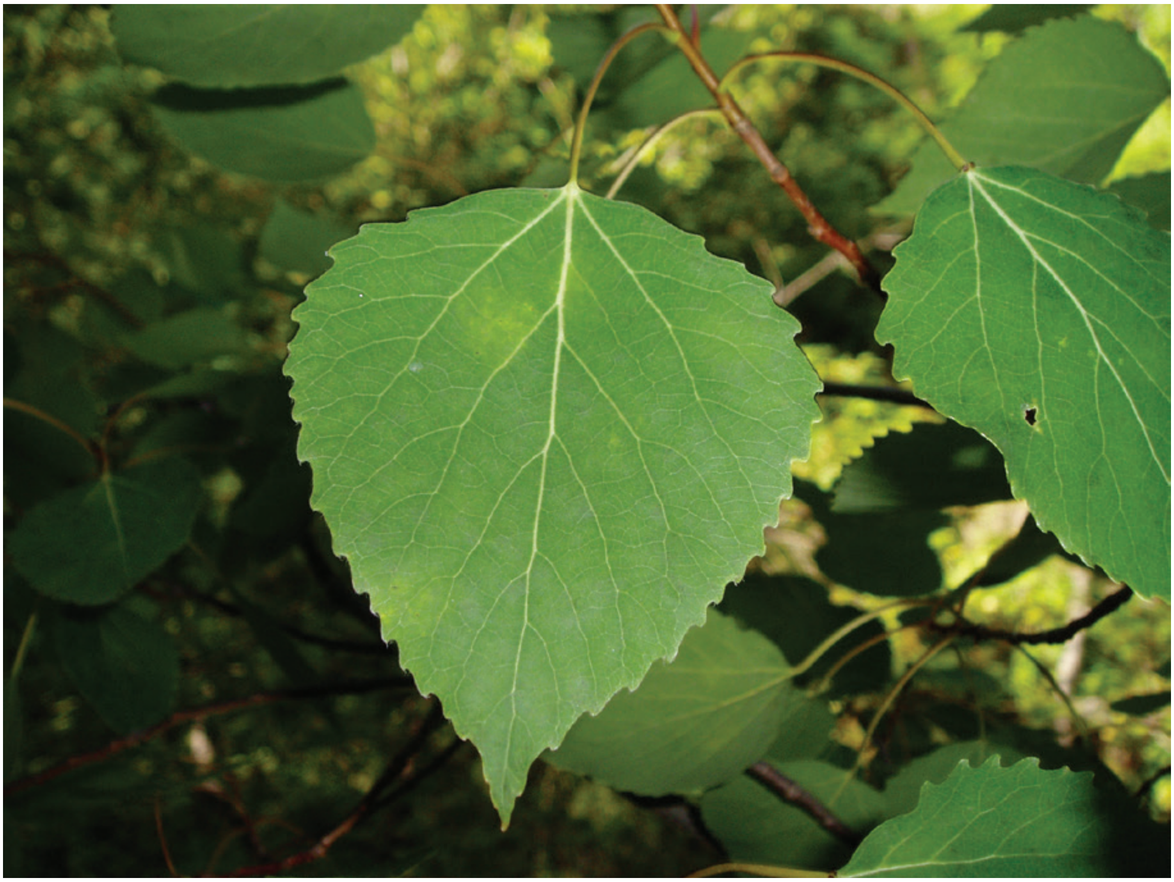


Many morphological characteristics for the Smith Falls aspens (below) show intermediate traits between the parent species, including the shape and number of teeth on the leaf margins and the degree of leaf and bud pubescence. Quaking aspen (*Populus tremuloides*) is shown at top left, bigtooth aspen (*P. grandidentata*) at top right.

When we began, it was immediately clear that the aspens at Smith Falls bear a great resemblance to quaking aspens. They have lovely white stems and dark green, heart-shaped, finely toothed leaves. They grow in clumped stands, indicating spread by rhizomes, with no singletons off on their own. We found these trees growing in a string of ten stands extending along the Niobrara River Valley, from Nature Conservancy holdings in the east to private property in the west. The stands in between these two locations are one of the crown jewels of Smith Falls State Park and are well known to its many visitors, who also come to raft the Niobrara River, camp out along its banks, and see the eponymous waterfalls. The aspen stands are confined to the cool, north-facing banks of the river, and they're undeniably beautiful trees. But, as aspen fanatics, we agreed with what we'd already heard about them: they seemed somehow different than the quaking aspens so familiar to us in Minnesota. Their bark, though light-colored, seemed rather green, and their leaves were rather large, with fewer and larger teeth, compared to a typical quaking aspen. Indeed, these trees had long been held by local botanists and natural historians to be hybrids between locally rare quaking aspen and bigtooth aspen—a species whose eastern range edge is currently estimated to fall around 375 miles (600 kilometers) to the east, near Ames, Iowa.

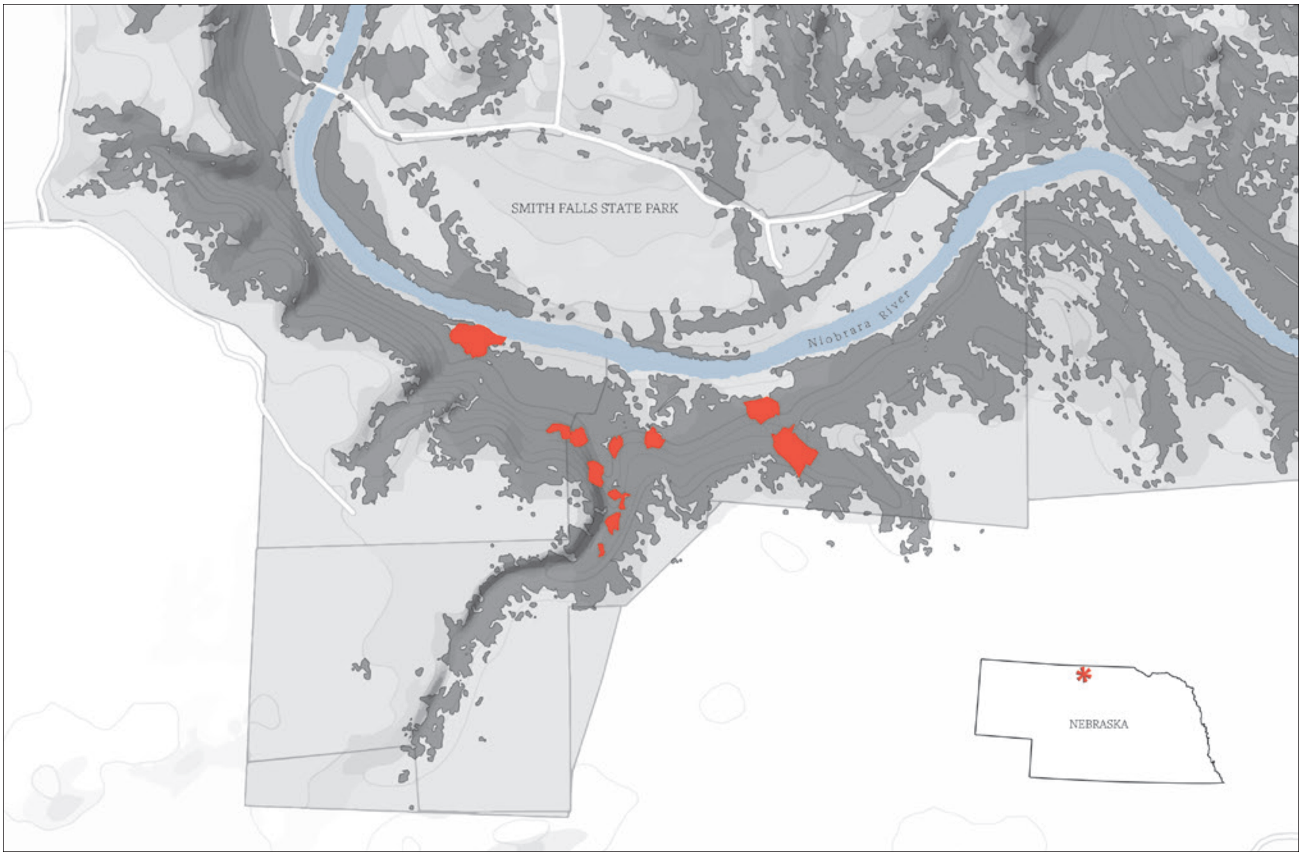
We knew that quaking and bigtooth aspen hybridize naturally within their range—renowned forest ecologist Burton "Burt" Barnes's seminal work documented many such stands in Michigan (1961)—but the thought of this hybrid having occurred naturally so far outside the distribution of one of its putative parental species struck me, at least, as somewhat scandalous. Aspen pollen is wind-distributed and can travel long distances, but there is no evidence of successful pollination events occurring when around 375 miles separate male and female plants. As such, I expected that the reputation of the Smith Falls aspens as hybrids was nothing more than understandable wishful thinking. After all, bark and leaf traits can be plastic, and a more parsimonious explanation of the unusual appearance of the Niobrara trees was that they were simply an unusual, isolated stand of quaking aspen. So, an important first step in our research would be to compare the genetics and morphology of the Smith Falls aspens to that of known quaking and bigtooth trees.

Our research group collected leaf samples, from which we could extract DNA, from all ten stands of Smith Falls aspens. We also dug up rhizomes to produce cloned suckers and planted these suckers in a common garden at a research station in Minnesota. There, we could perform experiments on them without harming the precious Niobrara trees. For the sake of comparison, we also drove all over the Midwest, collecting leaf and rhizome samples from quaking aspens in the Black Hills of South Dakota and the Sandhills of Nebraska, from bigtooth and quaking aspens along their western range edge in Minnesota and Iowa, and from both species within the interior of their distributions in Minnesota and Wisconsin.

Our assessment of the genetics and physiology of the aspens took place over two years at the University of Minnesota campus. We used microsatellite genotyping—the same technology that allows for DNA fingerprinting in humans—to understand which trees we had sampled were distinct individuals and which were clones. This work, as well as sequencing of parts of our sampled trees' chloroplast genomes, was possible thanks to the full genome for black cottonwood (*Populus trichocarpa*), which was produced by an international team of dozens of biologists led by Oak Ridge National Laboratory's Gerald Tuskan in 2006—the first whole genome project carried out for a tree species. In our physiological experiments, we pushed stems and leaves from our common garden trees to the brink. We measured them exhaustively, and we then dried them out and froze them to mimic climate change-induced drought and post-budbreak freezes. We also tracked their phenology—the timing of their leafing out and loss of leaves in our common garden.

An Ice Age relic

The results of our genetics work (Deacon et al., 2017) left me picking my jaw up from the lab bench. Our first finding struck an ominous tone: the Smith Falls aspens are shockingly



Genetic analysis of the ten aspen groves at Smith Falls (marked in red) revealed that only three genetic individuals occurred at the site. In some cases, these clones spanned opposite sides of the large canyon (and namesake waterfall) that bisects the park, suggesting aspens were once more widespread at the site.

undiverse. We are confident that, across all ten stands at the site, any given tree belongs to one of three genotypes. This means that three original seedlings produced through sex have given rise, through rhizome suckering, to all of the extant aspens in the area. We found genetically identical individuals growing on opposite sides of ravines and in stands separated by hundreds of meters. It appears, then, that these particular trees rely almost exclusively on asexual suckering for reproduction. More shocking still, at the nuclear level, the Smith Falls aspens shared genetic information with both quaking aspen and bigtooth aspen, confirming that they are a hybrid between these parents—a hybrid christened, appropriately enough, *Populus* × *smithii.* Evidence from chloroplast DNA suggested that bigtooth aspen, the species now not found until the middle of Iowa, was probably the maternal parent, with pollen coming from quaking aspen. Furthermore, patterns of genetic mixing we observed offer some support for the classification of these trees as F1 hybrids, meaning they are the first-generation offspring between two parents of different species, like mules.

Our study of leaves collected from common garden trees supported our finding that the Smith Falls aspens were in fact hybrids of quaking and bigtooth parents (Deacon et al., 2017). Use of a dichotomous key to distinguish between these species will often require inspection of the pubescence and margins of the leaves of the specimen in question. Quaking aspens tend to be glabrous with many small teeth on their leaf margins. Bigtooth aspens tend to be pubescent with fewer, larger teeth. Barnes's work on *Populus* × *smithii* tells the same story. Though we documented many subtle differences between leaves of the two species in our systematic analysis, our findings contributed to the current consensus: pubescence and tooth number are the best way to tell them apart. And leaves from *P.* × *smithii* trees grown in Minnesota from Nebraska-collected rhizomes were perfectly intermediate between their putative parents in these two traits.

Taken together, these findings suggest the rather shocking story that, at some point when both bigtooth and quaking aspen were locally abundant in the Niobrara River Valley—probably between three and six thousand years ago—the two species hybridized. Both parents went locally extinct (and bigtooth vanished from the entire region), but their hybrid remained, reproducing vegetatively through rhizomes rather than through flowers and seeds. Despite considerable environmental change—the climate in this region was warming and drying long before our present human-induced bout of climate change—these aspens hung on, perhaps shrinking in their distribution, but not disappearing from one small stretch of the Niobrara River Valley. As such, these aspens are a true relic of a past climate and a unique genetic treasure of the region.

Specter of climate change

Our grant from the National Parks Service enabled us to go beyond determining the genetic identity of these trees. We also used our common garden to study their disturbing demographic decline. State managers and conservationists had noted that existing aspens looked stressed and that new trees either were not sprouting or were quickly consumed by deer before outgrowing their reach. We wanted to understand the vulnerability of the Smith Falls aspens to two forms of physiological stress likely to be concomitant with climate change. The first is straightforward: climate change in the region is likely to lead to more arid conditions, imposing drought stress on the vulnerable, mesic species of the Niobrara River Valley. The second is less so: because the forces that cause this warming do not necessarily prevent late-winter cold snaps, even if spring temperatures arrive earlier, plants can leaf out in response to an early spring, then get hit with a freeze after budbreak. Such post-budbreak freez-

PHOTOS BY JAKE J. GROSSMAN

Each of the three aspen genotypes at Smith Falls is a first-generation hybrid, suggesting that the aspen trees found today at the site have descended through many generations of vegetative suckering, rather than seed reproduction, from the original hybrids. Vegetative suckering in aspens occurs via underground rhizomes, which the author showcases above.

"BUFFALO" BRUCE MCINTOSH AND WESTERN NEBRASKA RESOURCES COUNCIL

Large eastern red cedars (*Juniperus viginiana*) have encroached on the aspen groves at Smith Falls. This photo was taken before an intensive volunteer effort removed a large number of cedars, some shown in the midground of this forest. Ponderosa pine (*Pinus ponderosa*) rises in the background.

ing can range from damaging to catastrophic, potentially killing vulnerable tissues and leading to whole-plant death (Anderegg et al., 2015).

Our exploration of the aspens' vulnerability to climate change, currently in review, resulted in some bad and some good news. Unsurprisingly, given aspens' low level of drought tolerance, we found quaking, bigtooth, and hybrid aspens to be vulnerable to drought-induced cavitation, the formation of air bubbles in stem xylem. These bubbles, in quantity, disrupt waterflow in trees' vascular systems, like holes in a straw. They can, ultimately, lead to total hydraulic failure and tree death. Quaking aspen was slightly more vulnerable to this type of drought damage than bigtooth aspen, and their hybrid was intermediate. More generally, the hybrid aspens shared some drought-tolerance traits with quaking aspen, others with bigtooth aspen, and, in other cases, was intermediate between the two. But all three taxa showed a limited capacity to resist the challenges likely to occur in a warming and drying climate.

The story surrounding post-budbreak freezing was simpler and rosier. We froze growing stems and leaves at temperatures equivalent to and lower than those that aspens in Nebraska are likely to experience during March and April storms. They were not substantially injured by this, suggesting that drought threatens aspens in the Niobrara River Valley more than late-winter cold snaps. Interestingly, in our measurements of spring phenology—the transition from dormancy to budbreak—we also found that the Smith Falls aspens were intermediate between quaking and bigooth aspen. Our findings echoed previous work showing that quaking aspens break bud about a week faster than bigtooths; fittingly, we observed that their hybrid offspring tended to leaf out in between the two parental species. Yet, compared to other regional conspecifics, all three groups of aspens generally leaf out around the same time.

An aspen in a juniper's world

Though our determination that the Smith Falls aspens are in fact hybrids has proven fascinating and satisfying, thornier questions remain about their future. Locally, the Smith Falls aspens are being outcompeted by neighboring trees, especially eastern red cedars (*Juniperus virginiana*). Quaking and bigtooth aspens are tolerant of low-intensity fires but intolerant of shade. Fire exclusion has, therefore, been catastrophic for

"BUFFALO" BRUCE MCINTOSH AND WESTERN NEBRASKA RESOURCES COUNCIL

"Buffalo" Bruce McIntosh of the Nebraska Wildlife Federation leads a juniper removal initiative at Smith Falls.

aspens, whether at Smith Falls or more broadly across the West. Because cedars are fire intolerant but drought tolerant, they have capitalized on our modern tendency to suppress and prevent fires. Locally, managers have fought this cedar encroachment by instigating prescribed burns, clearing cedars, and creating barriers to deer browsing on aspens. As a result, suckering is on the rise in some stands, producing a new cohort of healthy aspens (Robertson et al., 2018). Yet cedar removal and prescribed burns are expensive and will need to be repeated periodically to keep aspens abundant at Smith Falls.

Globally, climate change is also likely to reshape the distribution of aspens across North America. Nebraska is expected to experience climate warming in the decades to come, in tune with the current global commitment to three to four degrees of warming. And though rainfall in the region will likely remain stable in absolute quantity, rain and snow will fall more sporadically, producing longer and more frequent periods of drought. None of this is good news for aspens in the region. Given historical changes in the distribution of quaking and bigtooth aspen, observations colleagues and I have made suggest the Smith Falls aspens will encounter a greater risk of climate-induced extirpation in the Great Plains than they have faced since the end of the last Ice Age.

We might ask, then, what the future holds for the Smith Falls aspens and for other glacial relics in the region. The answer to this question depends on management. Stands of quaking aspen, paper birch (*Betula papyrifera*), and other drought-sensitive trees can probably be protected through active steps to shield them from direct climate stress and competition from more drought-adapted neighbors. In addition to prescribed burns, possible management practices include removal of competitors, use of exclosures to reduce grazing, targeted planting, and conservation of local groundwater. For species such as the aspens, which can be more easily propagated through rhizome cuttings than from seed, collection of rhizomes and propagation of suckers represents one pathway toward conservation of unusual, threatened germplasm. At present, private individuals and institutions may be able to assist with the migration of the Smith Falls aspens by purchasing commercially available nursery stock. Faller Landscape, in York, Nebraska, presently sells clonal trees produced through suckering from

"BUFFALO" BRUCE MCINTOSH AND WESTERN NEBRASKA RESOURCES COUNCIL

The fate of the Smith Falls aspens under climate change will likely parallel the fate of other drought-intolerant populations in the region, including this grove of quaking aspen (*Populus tremuloides*), south of Smith Falls.

rhizomes collected at the site (marketed under the cultivar name 'Ice Age').[2] More broadly, any efforts to stabilize the global climate, if our society is willing and able to undertake them, will also benefit Midwestern aspens, among many other species.

Hopeful monsters or dead ends?

Like other natural hybrids, the Smith Falls aspens have been heralded, at least locally, as uniquely adapted to their surroundings. It is tempting to assert that these trees, by virtue of their longevity, may illustrate one strategy for persistence in a warming, drying climate. Yet findings from our research do not support this narrative. Indeed, these hybrids are unique, and worthy of study insofar as they constitute an evolutionarily unusual relic from a past climate. But as noted above, these trees represent essentially three genetic individuals that have probably been cloning themselves for thousands of years. Though we have very recently received second-hand confirmation that the trees do flower in some years, we do not know the sex of each clone, or whether their flowers are fertile. Genetic evidence certainly suggests that no new trees have been born from seeds at the site for a very long time. And the Smith Falls aspens are beset by environmental challenges ranging from the hyperlocal to the global. Unfortunately, the Smith Falls aspens may simply have survived by demographic good fortune, constituting an evolutionary dead end, rather than a way forward.

Yet this is a rather pessimistic view, and, having grown rather fond of the aspens at Smith Falls during my time working with them, I think their conservation is justified. As unusual hybrids that have persisted despite millennia of climate change—whether by chance or due to some particular adaptation we did not measure—they represent a potential genetic resource. As such, they may be candidates for assisted migration: transplantation from their current, imperiled location to one that will be more appropriate in the coming centuries of a climate determined by human-induced changes. Propagation of these trees in cooler and wetter climates well within the current ranges of their parent species might allow them to flourish while also buying time for intentional propagation of second-generation hybrids through breeding with other *Popolus* × *smithii* or backcrossing.

Regardless, we would be wise to remember that the story of evolution in response to a warming climate has occurred many times in the history of life, and it often produces messy stories like that of the Smith Falls aspens. What appear to us to be non-adapted (or even maladapted) trees may hold the key to surviving and thriving in a future climate. After all, the common ancestor of modern aspens and willows had likely evolved during the earth's last period of extreme warming, some fifty-five million years ago, when the tropics extended up to the North Pole (Manchester et al., 2006). Though the fate of quaking and bigtooth aspens and their hybrids is uncertain, the aspen lineage is likely to survive contemporary climate change. And so, whether hybrid aspens are best thought of as hopeful monsters or evolutionary dead ends is ultimately unknowable. But as an unlikely yet arguably successful hybrid myself, I'm inclined to give them the benefit of the doubt.

Acknowledgements

The original research reported in this article was conducted collaboratively at the University of Minnesota—Twin Cities with Jeannine Cavender-Bares, Nick Deacon, Anna Schweiger, and Isabella Armour. We were funded by National Park Service grant #191779 to Jeannine Cavender-Bares, Mark Dixon, and Molly Nepokroeff. Jeffrey Carstens, a horticulturist and curator of woody and herbaceous plants at the USDA's North Central Regional Plant Introduction Station in Ames, Iowa, played an absolutely essential role in guiding our collections of Midwestern aspens, especially along the species' range edges in Iowa. "Buffalo" Bruce McIntosh of the Nebraska Wildlife Federation and Joseph Zeleznik at North Dakota State University also provided essential help with collections in Nebraska and northern Minnesota, respectively. Three photographs in this article came from the video "Fighting for Survival: The Ancient Aspen of the Niobrara Valley," produced by "Buffalo" Bruce McIntosh, Rod Jensen, and The Great Plains Motion Picture Company.

Notes

[1] It should be noted that the chimaeras resulting from the almost unbelievable process of interspecies grafting (e.g. apples, pears, grapes, roses, citrus, mangos, stone fruit, and others, not to mention the introduction of certain porcine organs into human bodies) certainly give more integrated hybrids a run for their money in the realm of public interest.

[2] Aspen enthusiasts can also purchase from them a very robust and aesthetically pleasing quaking aspen genotype, 'NE Arb', which was collected from a now-extinct stand elsewhere in Nebraska.

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Jake J. Grossman is a Putnam Fellow at the Arnold Arboretum.

ELLENWOOD, J. 2019. ROAMING THROUGH RANGES: THE EVOLUTION OF TREE SPECIES DISTRIBUTION MAPS IN THE UNITED STATES. *ARNOLDIA*, 76(3): 14–27

Roaming through Ranges: The Evolution of Tree Species Distribution Maps in the United States

James Ellenwood

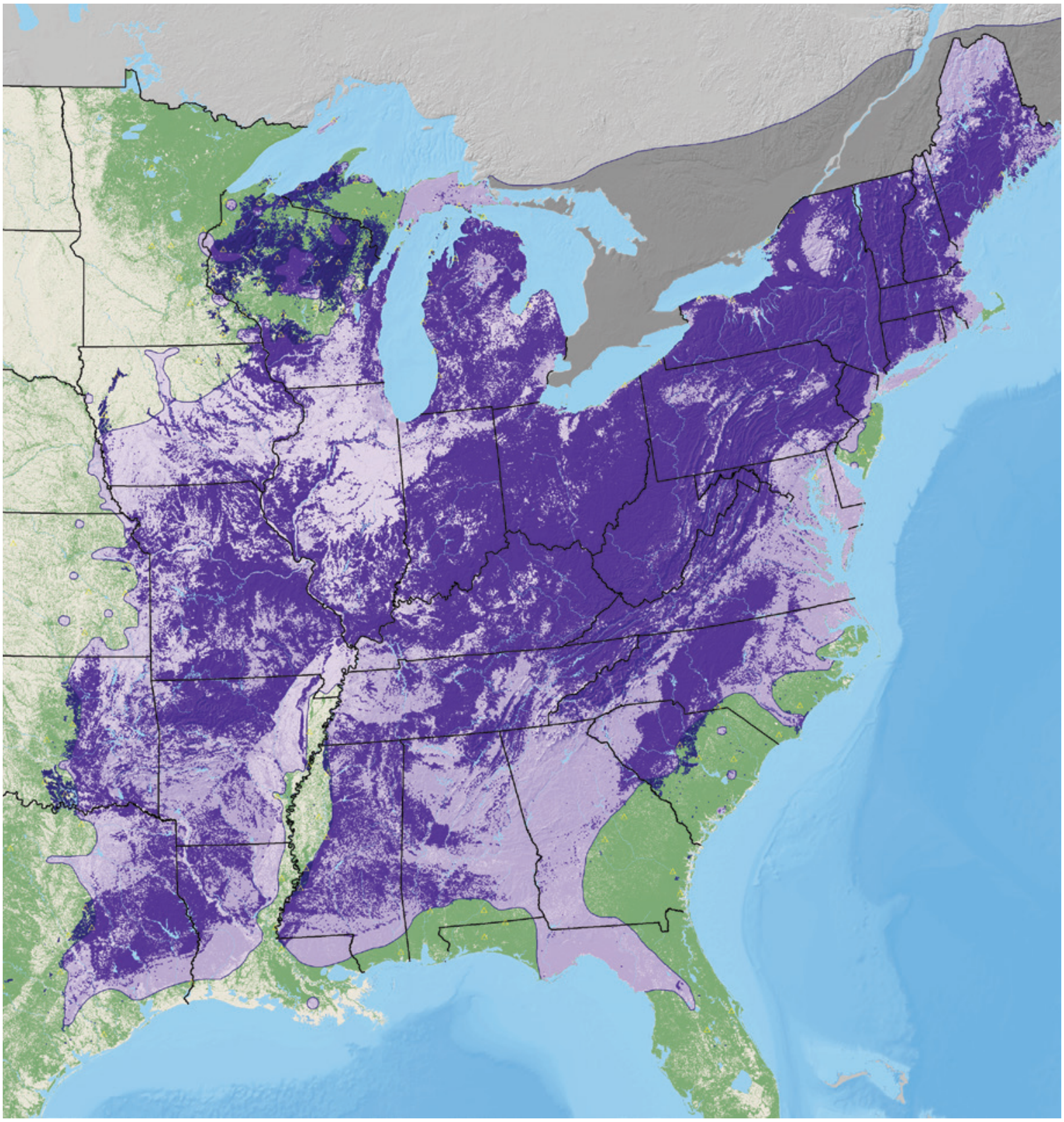
As a teenager, in the 1970s, I traveled with my siblings across the United States and Canada on a few multi-week road trips, camping and visiting National Parks and Forests. Along the way, I became fascinated by how different trees grow in different places—the tall, narrow-crowned Engelmann spruce (*Picea engelmannii*) found in the high elevations of the northern Rocky Mountains (which were still snow packed in the middle of June) and the incense cedar (*Calocedrus decurrans*) showing off its brilliant red bark on the western slope of the Sierras. The local tree species, I realized, were as distinct as the terrain—patterns that emerged over millions of acres and thousands of miles. The quest for adventure and the desire to see the natural world drove my ambitions, facilitated by recently completed interstate highways and a personal automobile. Ecological patterns that were once relatively difficult to see now emerged, much like the transition from still frames to movie frames, via easy roadside stops to get into the wilds.

Around this exact same time, these fundamental biological patterns were being synthesized into a comprehensive set of North American tree distribution maps by a botanist at the United States Forest Service named Elbert Little Jr. These maps were published in a six-volume set, collectively titled the *Atlas of United States Trees,* which covered around 720 species. Each map included shapes that represented the maximum extent of the distribution for a single species. Little and his collaborators developed these by drawing an outline around locations obtained from numerous published and unpublished sources, as well as personal knowledge. For decades, Little's maps have served as the definitive source for this distribution information. I referenced them as a student at the State University of New York's College of Environmental Sciences and Forestry in the early 1980s. And digital reproductions of Little's maps are now included on the Wikipedia pages for most—if not all—of the tree species that he documented.

In 2007, however, I began working with colleagues at the United States Forest Service to project the potential for forest mortality due to insects and diseases fifteen years into the future. This involved building thousands of models based upon remotely sensed imagery, environmental variables, and observations from field plots. After many trials and iterations, we recognized a need to bound the modeled maps by known tree distributions, but we knew that Little's maps couldn't be used for this type of analysis. For instance, if we were attempting to understand the threat of emerald ash borer (*Agrilus planipennis*) on populations of white ash (*Fraxinus americana*)—a widespread forest species in eastern North America—Little's map would suggest that white ash was equally prevalent in New York and Illinois, given that both states fall entirely within the range. Yet New York is widely forested, while Illinois is extensively cultivated. As a result, white ash populations would be much more fragmented in the western portion of its range, and Little's maps did not reveal this trend. Clearly new information was needed.

Original Maps

The history of mapping North American tree distributions is an ongoing narrative of collaboration on a national scale, but the evolution of these maps also reveals how cultural values (and even politics) factor into seemingly straightahead descriptive botany. My team began working on new distribution maps because of environmental concerns about the globalization of insects and diseases, an issue that wasn't remotely part of the scientific consciousness in 1880, when Charles Sprague Sargent, the founding director of the Arnold Arboretum, was leading an initiative to describe and inventory



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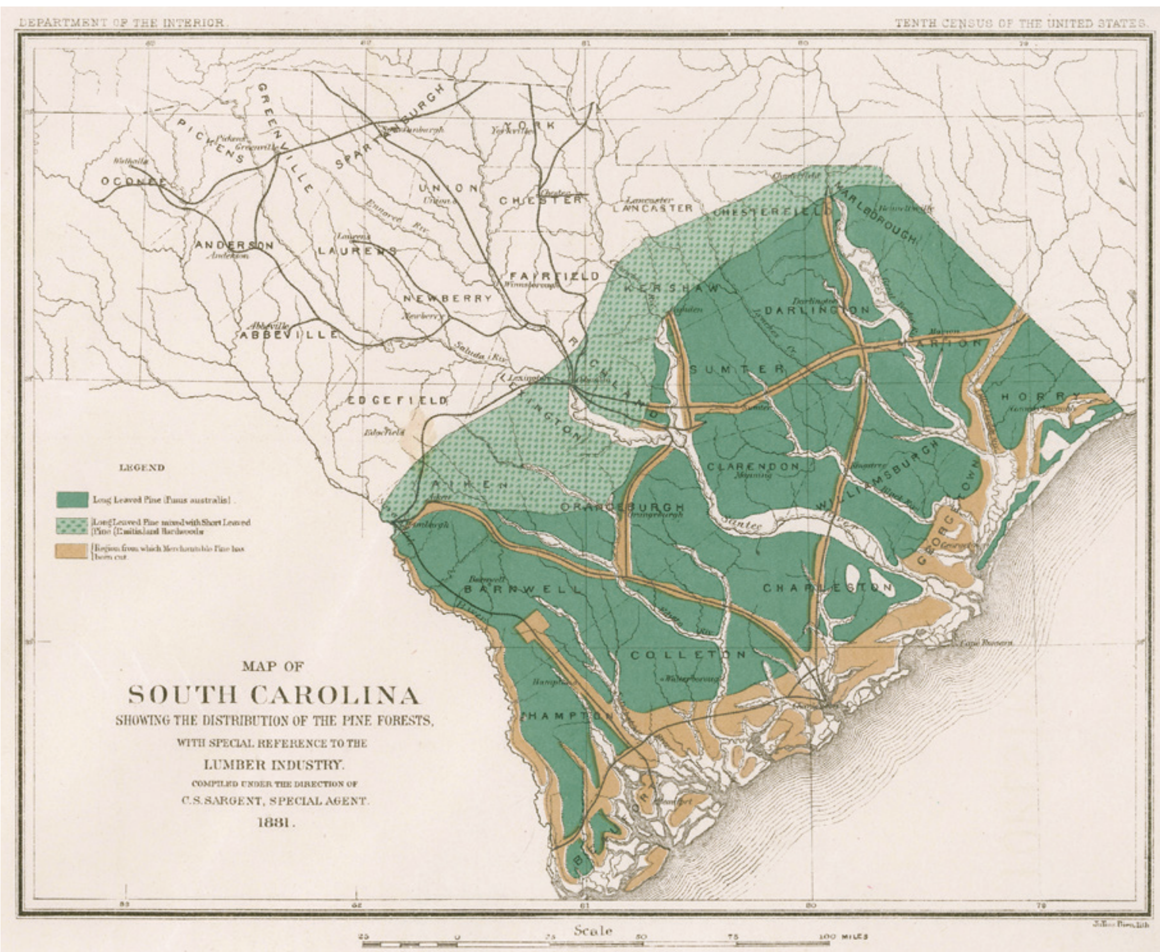
This map for white ash (*Fraxinus americana*), published in the *National Individual Tree Species Atlas* (2015), compares a classic distribution prepared by Elbert Little Jr. (light purple) with a new modelled distribution (dark purple).

forested landscapes for the 1880 United States Census. Rather, at that point in time, the primary driver for this kind of distribution mapping was related to economic interests.

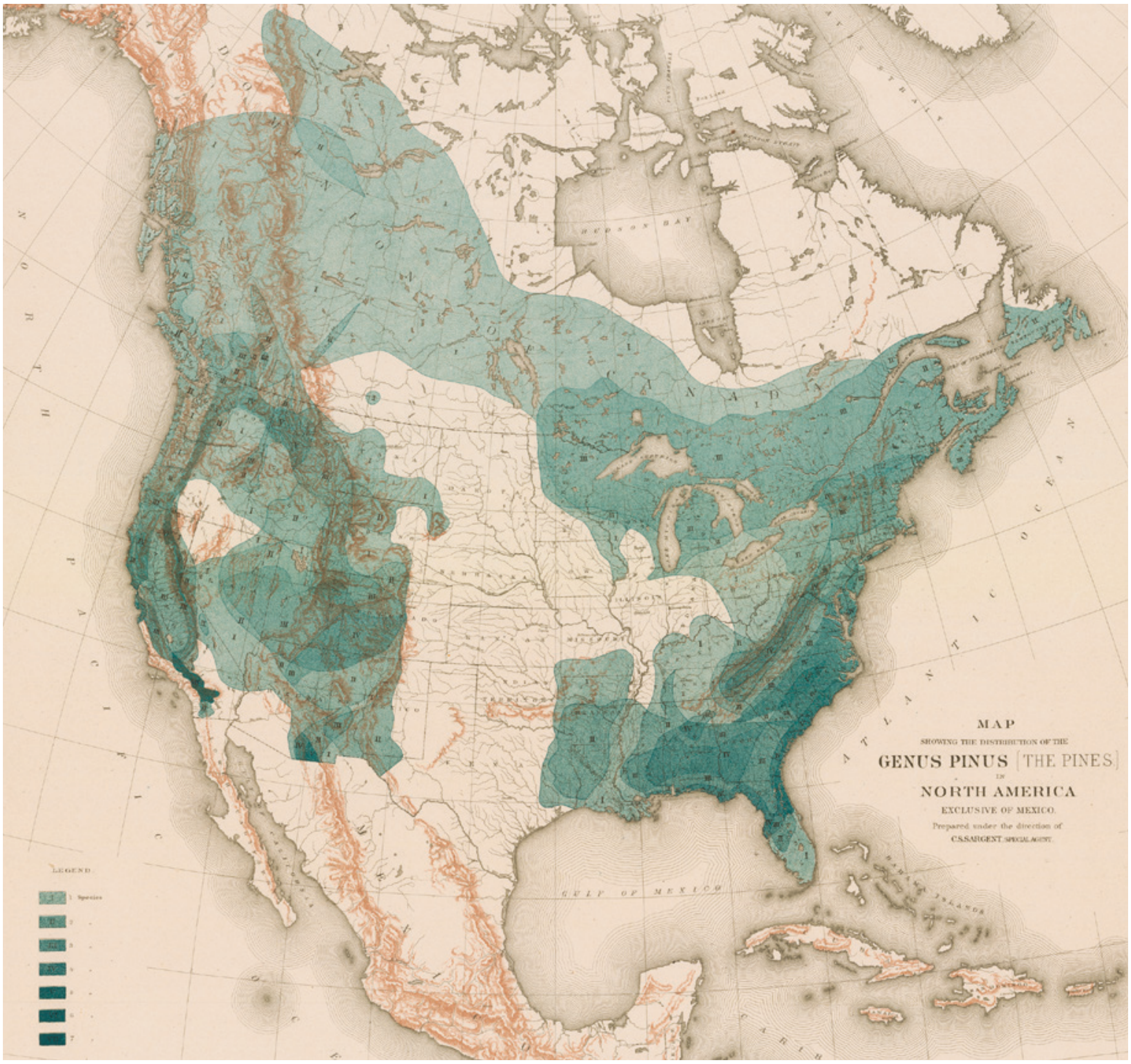
Sargent compiled information for about 412 tree species, which appeared in a voluminous final report, published in 1884. Some of this information came through personal field observations, but Sargent also enlisted the support of a team of botanists and natural history enthusiasts who traveled through specific regions, reporting on the composition of the forests. Most of the resulting distribution information was text-based, but the report also included several types of maps: One set showed the extent of forested landscapes for individual states. Another set, included as a large-format portfolio, showed the distribution of genera, like pines (*Pinus*) or oaks (*Quercus*), on a continental scale, with monochromatic shading used to indicate the number of species in each location. All the maps were prepared by Andrew Robeson, Sargent's brother-in-law.

It is particularly interesting to look at how the census report renders a single economically important species, like the long-leaf pine (*Pinus palustris*). Sargent called the species "a tree of first economic value" and described a distribution that spanned from southeastern Virginia, through the Gulf states, and into eastern Texas, "rarely extending beyond 150 miles from the coast." On maps of the corresponding states, long-leaf pine was singled out for more detailed representation, and the maps also indicated "regions from which Mercantile Pine has been removed." Farther west, individual species were not tracked on the state maps, which instead showed the density of forests. Likewise, the supplementary map for all pines indicated only the density (essentially a heatmap) rather than showing the ranges for individual species. As such, if someone wanted to determine the scattered range for something like the whitebark pine (*P. albicaulis*), which favors subalpine regions in the western mountains, the text-based descriptions would have been the best resource. Of course, individual species maps would have required many more



ARNOLD ARBORETUM ARCHIVES

Charles Sprague Sargent's 1884 census report included forest maps for individual states. For South Carolina, the distribution of two species of long-leaf pine (both now recognized as *Pinus palustris*) are shown in green. Commercially harvested forests (shown in burnt orange) emanate from the coast and along transportation corridors.



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The census publication included sixteen large-format maps, including one showing the density of pine species. The darkest shading, shown only in southern California, indicates that the census recognized seven pine species in that area.

field observations than were currently available. A large region in the center of the Idaho census map was still labelled "unexplored," which now offers an evocative reminder of this information scarcity.

While the census project was nearing completion, Sargent simultaneously chaired an initiative to preserve woodlands in New York's Adirondack Mountains from deforestation, which culminated in the establishment of Adirondack Park—the country's first state forest preserve—in 1885. It is clear that Sargent was aware of the utilitarian value of the census project, given that more than two hundred pages of the final report were devoted to the material properties of wood derived from each species, yet mapping the forests also revealed the finite dimensions of a resource that had once seemed limitless, potentially setting the stage for subsequent conservation and preservation movements.

Developing Detail

While the census report provided a useful synthesis of information known at the time, by 1898, George Bishop Sudworth, a dendrologist for the United States Department of Agriculture's Division of Forestry, articulated the need for a more comprehensive and up-to-date treatment of distribution information. "The army of professional and amateur botanists engaged in botanical research are yearly bringing to light new facts, which are constantly enlarging our understanding of the geographical distribution of trees and other plants," Sudworth wrote in the first edition of his *Check List of the Forest Trees of the United States: Their Names and Ranges,* which was published that year. The checklist included short descriptions of the ranges for five hundred species, but he knew that much more collaborative work was still needed.

The 1898 checklist ultimately presaged Sudworth's lifelong effort to develop better species distribution maps. Significantly, in 1913, Sudworth published an atlas for North American pine species, which was intended to be the first volume of a series covering all native trees. These maps represented a significant step towards the familiar appearance of distribution maps today, with each species rendered on a single map showing the entire range. Sudworth even showed the distribution of relatively sparse species like the whitebark pine, with green marking that followed the narrow elevational bands along mountain ranges. Given the scale, a reader would have difficulty in seeing the range for whitebark pine without the use of visual aids such as a magnifying glass, but the effort suggests the amount of detailed field observation that went into the project.

Sudworth attributed the success of his maps to work being conducted by the new United States Forest Service, established in 1905, which provided invaluable "unpublished field notes, unrecorded observations, and reports of Forest Service officials engaged in the exploration, surveying, and administration of the 163 National Forests now established." Sudworth's assistants compiled information from these sources, along with state floras and other resources, on cards for each species, and these annotations were plotted on a map of North America. Sudworth knew that the simplicity of maps far exceeded the usefulness of even the most detailed text, yet his volume on pines was the only portion of the atlas ever published.

The explanation for Sudworth's discontinuation of the atlas project might be intuited from the publication of subsequent bulletins that included maps of select tree species (including additional conifers) in the Rocky Mountains. Given that much of Sudworth's field information arrived from the National Forests, which were almost entirely located in western states (at the time), it makes sense that the maps would ultimately share the same regional emphasis, with special attention given to species that were of economic importance.

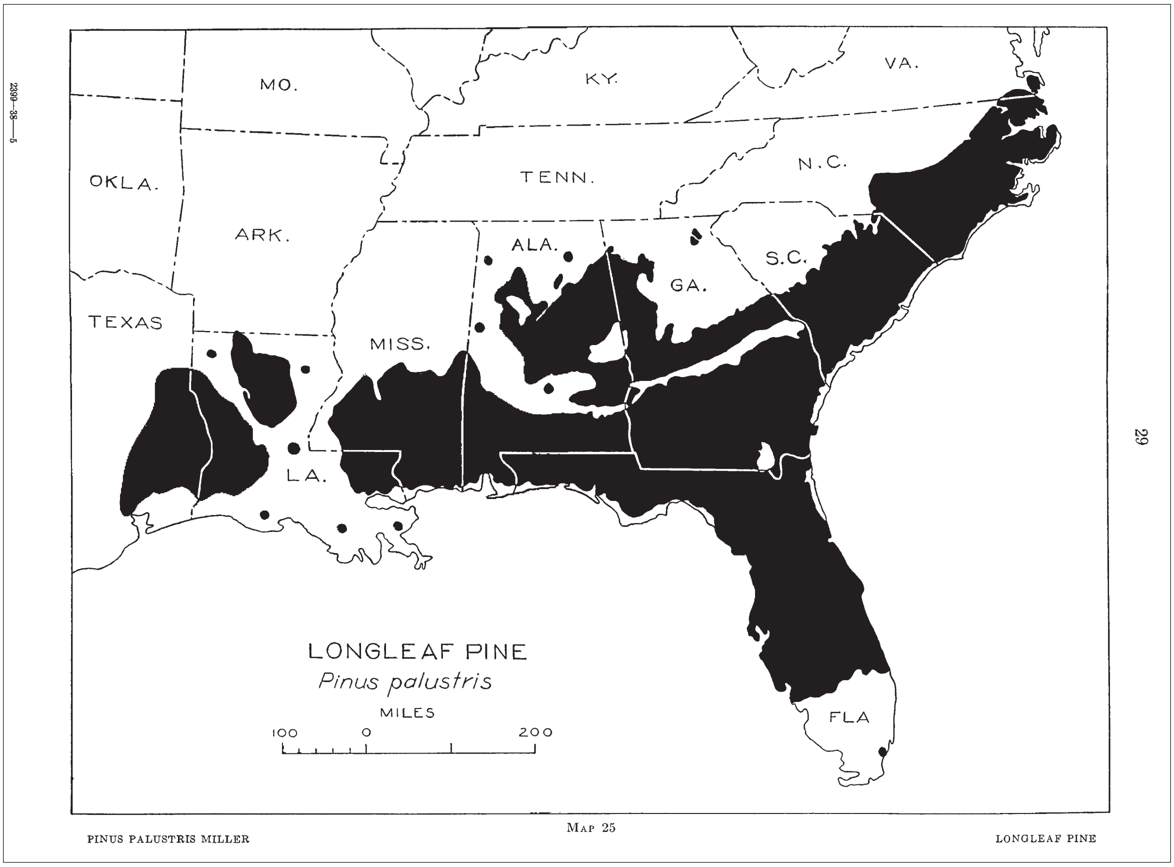
In 1927, the year of Sudworth's death, he published a revised checklist of North American tree species, in which he briefly described the range for every known species at the time (adding more than three hundred taxa to his original checklist). Sudworth knew the information would prove useful "not only among foresters, woodsmen, and wood users, but also in forest schools and other educational institutions." At the time, he and an assistant were once again working on maps—with many complete but unpublished—but the effort was suspended as priorities shifted (perhaps related to the Great Depression).

Developing Breadth

Edward Norfolk Munns, the chief of the Forest Service's Division of Forest Influences, eventually returned to the work that Sudworth and his assistants had started. In 1938, he published an atlas covering 170 of the most important tree species, which he noted was "based very largely" on Sudworth's research, with many updated observations compiled by junior forester William W. Mitchell. Although the species representation was far greater than anything published in Sudworth's lifetime, critics suggested that the maps should have been shared with field botanists and foresters for additional corroboration, because to many working on the ground, errors were evident. Even so, the atlas was reprinted by popular demand.

Beyond utility for botanists, foresters, and "the manufacturer in search of raw materials," Munns also described new ecological and engineering implications for the maps, no doubt based on his early field experience studying the impact of wildfires on California watersheds.

George Bishop Sudworth's 1913 atlas included distribution maps for thirty-six species of pines. This map shows the scattered high-altitude distribution of whitebark pine (*Pinus albicaulis*)



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This detailed rendering of long-leaf pine (*Pinus palustris*) appeared in the 1938 atlas prepared by Edward Norfolk Munns.

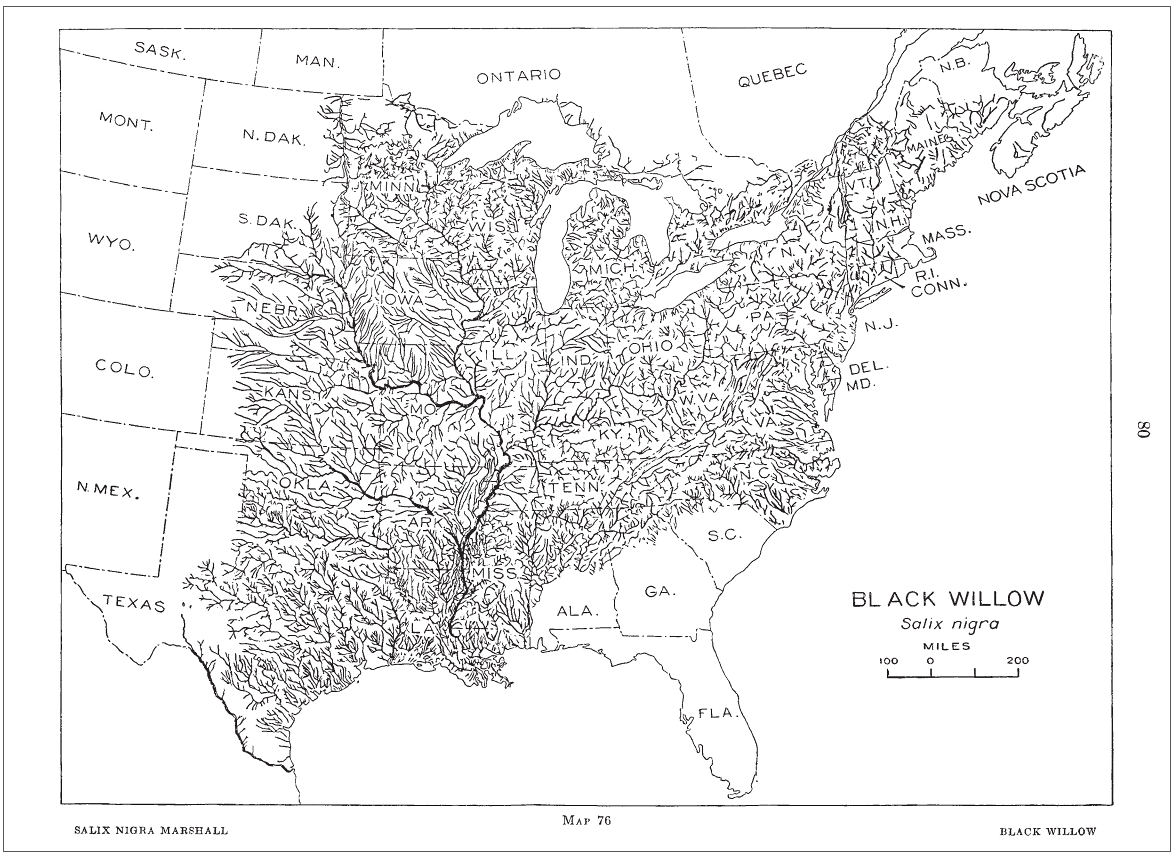
"[Forest distribution] is an essential element in erosion and flood control operations, and in land-use planning," he wrote in the introduction. "Indeed, present trends toward better planning and integration of land use are directing increased attention to forest cover, the species represented in it, and the possibilities of enlarging the contribution of forest land to community welfare." This, of course, may have been a suggestion that worked better on paper than in practice, but the statement represented an important expansion of what distribution maps could enable.

Ultimately, in 1942, a forest ecologist name Elbert Little Jr. was appointed as dendrologist for the Forest Service. Like both Sudworth and Munns (and myself), Little had spent a considerable amount of time at Forest Service field stations in the West, before taking his appointment at the national office in Washington. Little's continuation of the mapping project began with small generalized ranges for 165 forest species of economic interest, published in 1949. He later explained that the small size of the maps was due to practical and logistical reasons, given that it is easier to approximate an accurate range at a smaller scale. "Botanists, foresters, and other authors bold enough to summarize plant distribution records graphically may expect criticism instead of reward for their efforts," he wrote in a follow-up article in *Rhodora.* "It is far easier to detect a minor flaw along a boundary line than to prepare a better map." I learned this lesson very quickly in my own endeavors, to say the least.

Over the next two decades, Little and his assistants worked rigorously to expand the distribution data, sifting through more than three hundred sources, including unpublished card files in state herbaria and doctoral dissertations. Like Sudworth's maps, the reference points were then plotted onto a map of the United States or

North America. The first volume appeared in 1971, and the next five volumes appeared over the next ten years, ultimately covering more than seven hundred species of trees and major shrubs. When Little published on the distribution of trees in Alaska, he retained the individual reference points within the distribution outlines, but otherwise, the maps generally followed the classic form, with a simple outline drawn around all contiguous populations. This work still represents the standard reference for tree species ranges in North America today.

The first volume of the atlas also included nine semi-transparent overlays, nested within a cover pocket, which could be superimposed over the range maps. The overlays included features like "precipitation and rainfall," "plant hardiness zones," and "maximum extent of glaciation in the Wisconsin Glacial Stage." While the subsequent volumes did not include these transparencies, the originals could be used with two of the other volumes. If Munns, therefore, alluded to the possibility of using the distribution maps for something beyond a guide to natural resources, Little's transparencies indicated a genuine commitment to expanding the types of questions that could be raised with the maps. "They provide the basis for correlation studies of distribution of a species and the environment," Little wrote of the overlays (in the fourth volume). Moreover, as someone who began his career as a forest ecologist, Little saw a greatly expanding set of research questions that would benefit from the maps, including "such studies as classification, evolution, paleobotany, and genetics, and for the distribution of associated animals and plants, especially insects and parasitic fungi." Although the transparencies may seem simple compared to modern approaches, the effort to enable comparisons between tree



For many water-loving species, like the black willow (*Salix nigra*), Munns rendered the distribution according to rivers and streams.

species and environmental conditions represents a milestone development.

Once published, Little worked vigorously in trying to maintain an authoritative record for each individual species, even after retirement. A colleague of his related a story of visiting an area in Wisconsin in the 1980s where there was a rumor for the occurrence of a species that wasn't depicted in the atlas. Little brought his field maps, confirmed the sighting, and promptly penciled in the location. Eventually, the field maps were brought back to the office for inclusion in the authoritative maps. Little stressed the importance of continual maintenance. His coauthor on the second volume, Leslie Viereck, continued to maintain records for Alaska and produced a second edition, which included range adjustments, some species reclassifications, and an expansion to include significant shrub species. It was unfortunate that Viereck passed away in August of 2008, about a year before we started on the finer scaled species distributions.

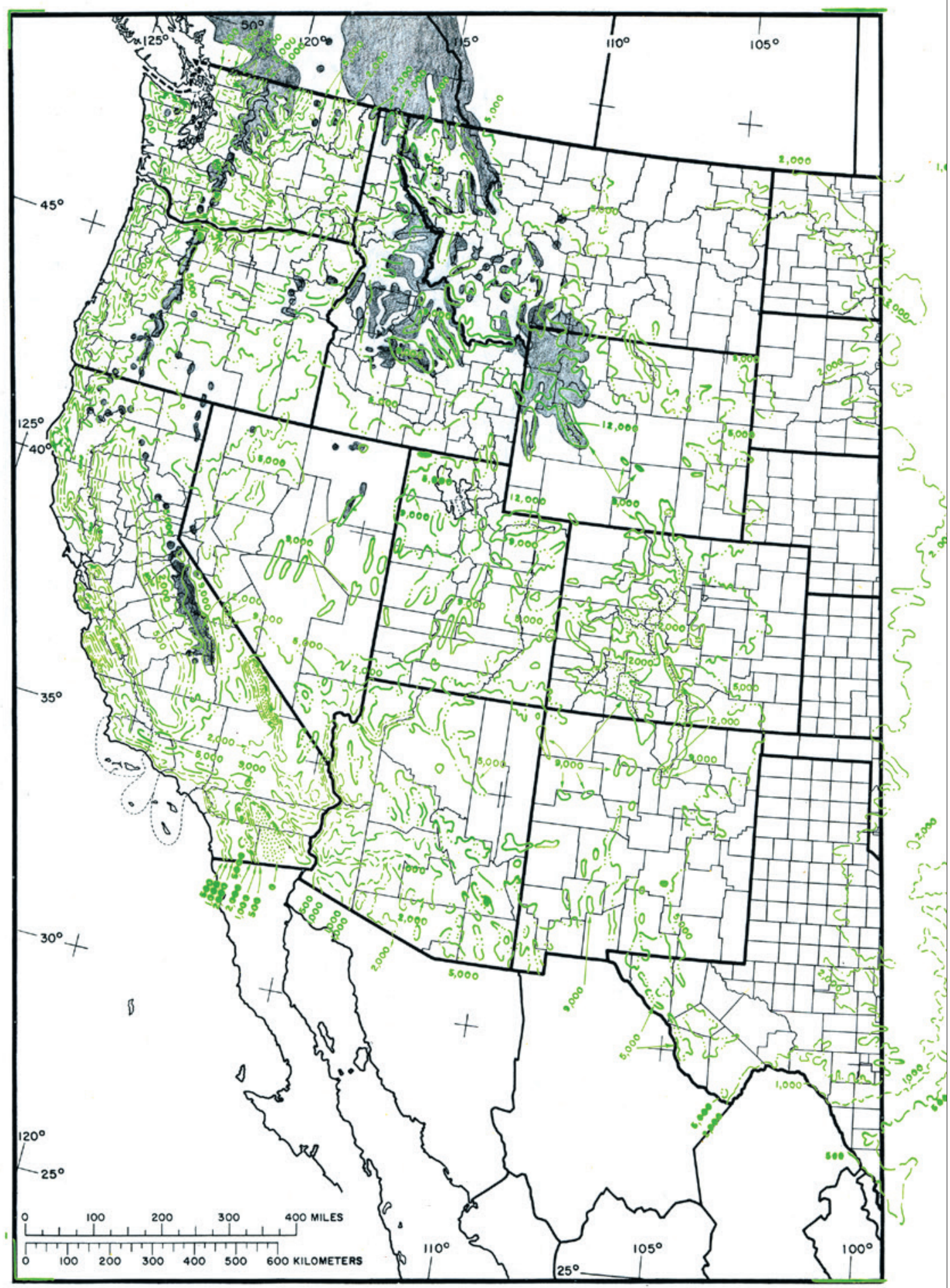
Modelling the Present

After Little retired from the Forest Service in 1975, the position of dendrologist was unfortunately abolished. In the ensuing decades, ecosystem classifications became the mapping priority. Communities of trees were identified as the dominant factors necessary for analyzing impacts of forest management, and distribution maps for individual tree species were no longer emphasized. With shifting priorities, staff changes, and a relocation of the National Headquarters, the whereabouts of Little's authoritative maps was lost through the ages. Although I have encountered people whose tenures overlapped with Little's, it is likely that the data have been forgotten, left in an attic, or moved to a storage facility at the Department of Agriculture's Greenbelt center or to a National Archives and Records Administration facility. If these data are recovered in the future, it would be important to appropriately curate them for further refinement and research.

In some disciplines, however, the need for better species maps became critical. Given practical considerations, Little was required to take inherent liberties when connecting a distribution outline around scattered dots, and the resulting shapes also failed to convey the density of forests. Moreover, the maps no longer represented the best information about the current distributions. Limitations like this are inherent to the mapmaking process. Even Sudworth, writing in 1913, noted the forests were changing faster than the maps could show. "Extensive and continued lumbering operations with attending forest fires have so changed, and in some cases exterminated, parts of the original stand of most of our pines," he wrote. "These maps, therefore, indicate only the general occurrence of species with the prescribed areal limits, and have no reference to the density or continuity of growth." Munns made the same point twenty-five years later, and Little echoed these concerns.

These limitations ultimately fueled my work with the Forest Service's Forest Health Technology Enterprise Team, where we needed to develop models to predict the risks associated with forest pests. We obtained current observations of 346 species that occur at Forest Inventory and Analysis field plots, as well as from other permanent plots managed by the National Forest System and the Bureau of Land Management. This amounted to more than 330,000 plots (and more than 1.2 million subplots). We linked this information to predictive layers pertaining to environmental variables like climate, terrain, soils, and satellite imagery. This dataset was then used to model individual species presence, as well as stand density, which was necessary for pest risk mapping. In the end, we successfully modelled the distribution of 264 trees sampled on these Forest Service plots, and as a by-product of that work, we published the *National Individual Tree Species Atlas* in 2015. Of course, this printed document will ultimately become a historical artifact, much like Little's volumes, given that the forests in the country will continue to change and transform in response to disease and insect pressure, climate change, habitat destruction, disturbance recovery, and any number of other threats (or boons), many still unforeseen.

The difference between the distributions shown on Little's maps and our models is often quite noteworthy, so our published atlas also



Overlay 3-W. Topographic relief. Contour lines at selected elevations. (Western United States.)
Map 43-W. whitebark pine, *Pinus albicaulis* Engelm.

ARNOLD ARBORETUM ARCHIVES

The first volume of Elbert Little Jr.'s *Atlas of United States Trees* (1971) included nine overlays that allowed for environmental analysis. In this case, a topographical overlay has been superimposed over the range of whitebark pine (*Pinus albicaulis*). Also note that the atlas included county borders.

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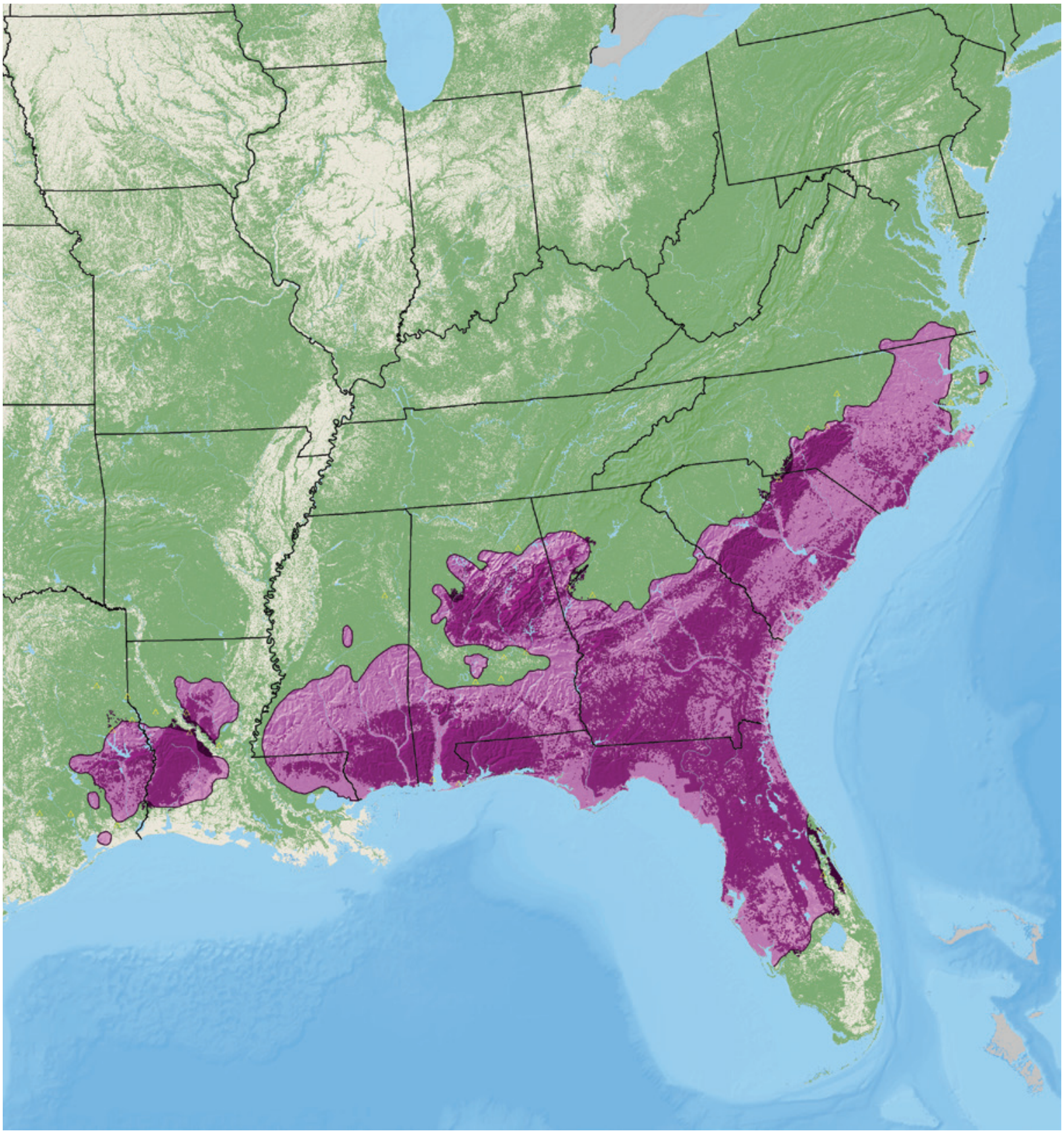


This map of long-leaf pine (*Pinus palustris*), published in the *National Individual Tree Species Atlas*, shows a smaller modeled distribution (dark purple) compared to the distribution outlines prepared by Elbert Little Jr. (light purple).

includes Little's outlines for comparison. It was my hope that this format would draw awareness to the ongoing need for studying these ranges—work that might require the oversight of a twenty-first-century Little (an authoritative steward of tree species distribution data)—however, even now, no specific authority is responsible for maintaining comprehensive distribution records. The United States Department of Agriculture's Natural Resources Conservation Service maintains the PLANTS Database, which has some degree of authority, although species distributions are only tracked at the county level, at best, which is adequate for general applications but not for applications in need of a finer scale.

For many species, like the long-leaf pine, comparison between the models and Little's maps suggests range contraction. The same is true for the whitebark pine. Both species are recognized as endangered, according to the International Union for Conservation of Nature, although for different reasons. The long-leaf pine was eventually disfavored by the forest industry due to its lengthy sapling ("grass") stage, and as a result, commercially managed forests were preferentially replanted with loblolly and slash pines (*Pinus taeda* and *P. elliottii,* respectively). The species is still threatened with continued habitat loss, although substantial restoration efforts are underway. Whitebark pine is currently most threatened by recent outbreaks of mountain pine beetle (*Dendroctonus ponderosae*), a native insect that has caused widespread mortality among western pine forests. In both cases, the models are critically important for monitoring current populations, as well as for projecting the future of these populations.

Other species, like the Osage orange (*Maclura pomifera*), however, show a dramatic range expansion. The range shown on Little's map is an upright column running through eastern Texas, barely extending into southern Oklahoma and Arkansas. Little wanted to show the original range for the species, before it had been widely planted as a living fence between agricultural fields in the Midwest. Because the species readily naturalized, our models, based on information about actual occurrence at field plots, shows a much wider range, with populations as far afield as western Pennsylvania. Our atlas also includes ranges for three nonnative species—tree of heaven (*Ailanthus altissima*), Chinese tallow tree (*Triadica sebifera*), and empress-tree (*Paulownia tomentosa*)—which have naturalized widely. Since these ranges weren't recorded in Little's atlas, this will provide invaluable baseline information for future management and research efforts.

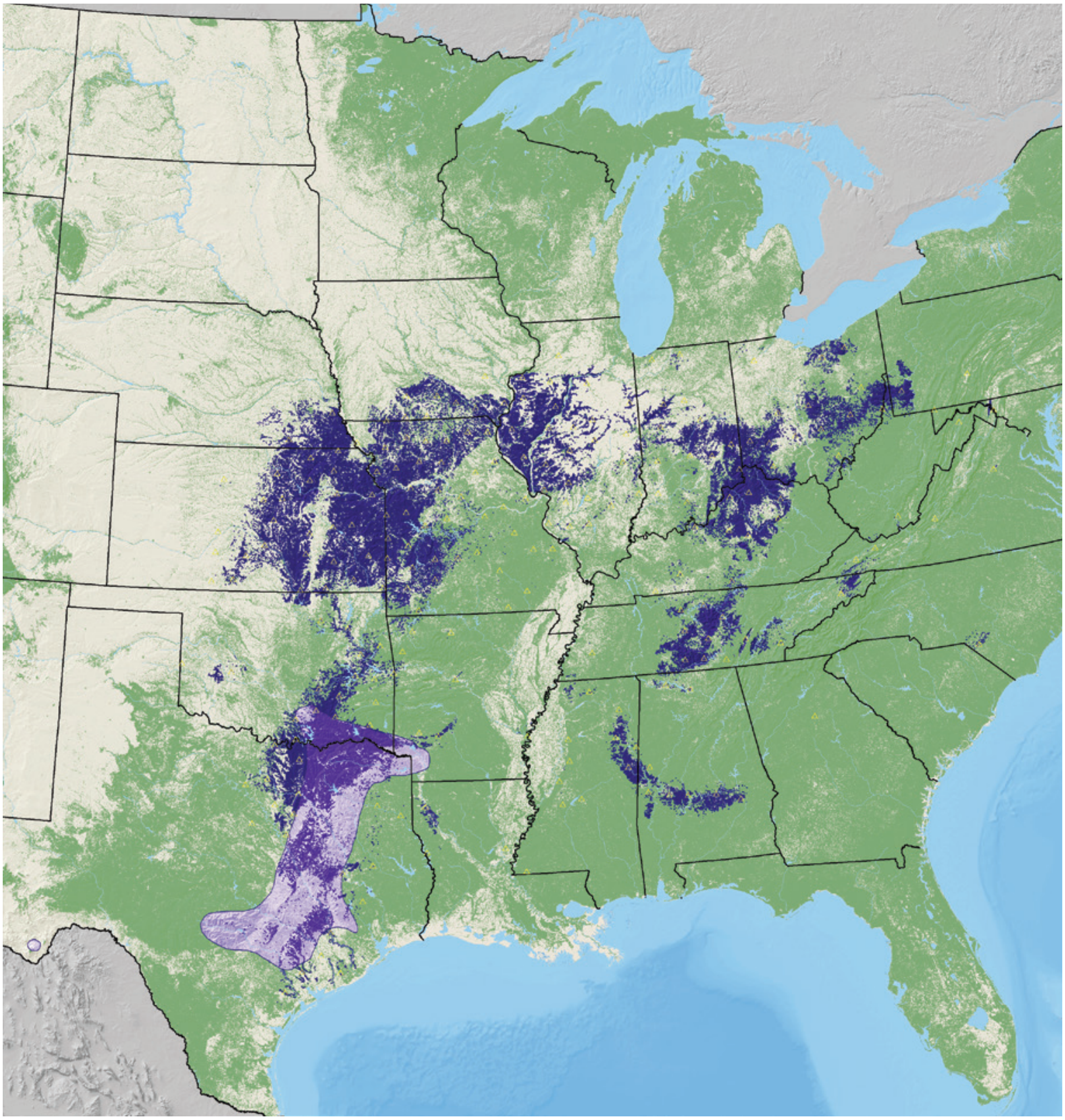
Changes to species classification can also result in significant changes to the distribution maps. The bristlecone pine, for instance, was separated into two species—Rocky Mountain bristlecone pine (*Pinus aristata*) and Great Basin bristlecone pine (*P. longaeva*)—which were easily separated based upon geographic data. Other species classification changes were not so easy. The Mexican pinyon pine (*P. cembroides*) was divided into two additional species, border pinyon (*P. discolor*) and papershell pinyon (*P. remota*), but the distributions were much more difficult to separate due the coincidence of the three species.

As the inventory is maintained, newer modeling techniques can improve the distribution maps for only the species measured on an inventory plot. Other naturally occurring species—often those with more restricted ranges in the first place—will need different data sources and greater effort to be developed.

Beyond Borders

While developing our models, we had the privilege of working with colleagues in Mexico to develop pest risk maps for Douglas fir (*Pseudotsuga menziesii*) and several key pines. Though we limited our investigation to eight species that had coarse climate and soils data, the permanent inventory for Mexico is designed much like the United States, and the potential exists to develop a complete set of species distribution maps for Mexico. (It should be noted that while 387 species were encountered within inventory plots in the United States, the Mexico inventory counted over 3,000 tree species.) Meanwhile, the resolution of our information does not carry into Canada, given limited access to the same amount of field data. Canada produced distribution maps for approximately ninety-three species, although they are of limited precision compared to the maps in the United States. At present, however, our own models don't extend north of the border either. In this sense, political relationships are often implicit in distribution maps, much as economic and ecological imperatives have manifest themselves throughout this ongoing history.

Given the nature of remote sensing, however, there is increasing potential to combine forest inventories to map complete species distributions, regardless of political boundaries. The North American Forest Commission is currently developing a combined database for Mexico, Canada, and the United States, and the success of a shared system like this was recently demonstrated in Europe. The European Union published the first systematic atlas of trees at the continental scale in 2016, which grew out of an effort to harmonize data within a continent-wide forest information system, established in 2013. Although the authors stressed the need for even more data (collected using more consistent methods and metrics), the resulting atlas is testament to the achievements possible with international collaboration. Moreover, the Food and Agriculture Organization of the United Nations asks all countries to assemble a National Forest Inventory every five years, and although the distribution data are relatively



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This map of Osage orange (*Maclura pomifera*), published in the *National Individual Tree Species Atlas,* shows an expanded modeled distribution (dark purple) compared to Little's distribution outlines (light purple).

coarse, efforts like this suggest the potential for a much more comprehensive set of tree species maps, especially in temperate regions where species diversity is less complex.

Taken together, these aspirations suggest the longevity of Sudworth's observations in 1898. "The geographical range of any of our trees must necessarily be an expression of the united efforts of all working botanists," he wrote, "for the unaided diligence of one man's lifetime could never carry his search and study into all of nature's hiding places for even trees alone." Since the completion of the *National Individual Tree Species Atlas,* many changes have occurred that would enhance future modeling efforts. Modeled maps now have the potential to be dynamic and adaptive, but they still require the collaborative vision of botanists, foresters, and plant ecologists in the field, now and for generations to come.

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James Ellenwood is the National Program Lead for Monitoring, Remote Sensing, and Geospatial Analysis Research at the United States Forest Service.

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Taiwan Dispatches

Ernest Henry Wilson

In March of 1919—one hundred years ago—Ernest Henry Wilson returned from his sixth and final plant collecting expedition to eastern Asia. The trip had begun in Yokohama, Japan, in January of 1917, and he traveled widely, tracing his way from Okinawa to Korea, even touching briefly into China. In early 1918, he sailed for Taiwan, where he was enamored with the subtropical conifers. According to his own tally, he collected more than seven thousand herbarium specimens, and he would return for seed in the fall. Taiwan, then known as Formosa, had been occupied by Japanese troops for more than two decades. Wilson's travels were conducted with a Japanese botanist named Ryozo Kanehira, and initial collecting locations were recommended by Bunzo Hayata, a botanist at the Imperial University of Tokyo. The following excerpts come from Wilson's handwritten letters to Charles Sprague Sargent, the director of the Arnold Arboretum. Italics have been added.

JANUARY 17, 1918 | YOKOHAMA, JAPAN

My arrangements are all completed for the trip to Formosa & I leave here in the morning. I plan to stay in Formosa for about ten weeks if the money in hand be enough to enable me to do so.

JANUARY 25, 1918 | TAIPEH, FORMOSA

Just a note to let you know that I have reached Formosa & that everything is favorable to a successful visit. I arrived here on the 22nd & leave tomorrow (26th) for Arisan where the giant trees are.… The officials, one & all, promise every assistance & there is no doubt but that they mean it. A Mr. Kanehira, who speaks English & is one of the heads of the forestry department, has been detailed to accompany me to Arisan & will probably go elsewhere with me also. He is a very nice fellow & I fancy will make a genial companion.… It is now eleven years since I begged some scraps of *Taiwania* [a monotypic member of the cypress family (Cupressaceae)] from Hayata & got promises, which were never fulfilled, of more material of Formosan conifers. I intend now to make up for lost time & our Herbarium shall possess its compliment of Formosan conifers ere I am through.

FEBRUARY 16, 1918 | TAIPEH, FORMOSA

I am back from the trip to Arisan & have but one regret which is that you too were not present to enjoy the forests & the giant trees. I had expected much but what I saw far exceeded my expectations: the forests are easily the finest & the trees the largest I have ever seen.… The country is very steep & savage & travelling over it is hard work. Thanks to a light railway & courtesies extended by the government things were made as easy for me as they possibly could be made. The weather on the whole was good though two consecutive days of rain & sleet & many foggy afternoons were a hinderance. I collected over twelve hundred specimens, representing about two hundred species, & took six and one-half-dozen photographs … The *Chamaecyparis formosensis* [an endemic false cypress] is the largest tree being sometimes

Wilson was awed by the enormous conifers near Mount Arisan. On February 1, 1918, he photographed *Taiwania cryptomerioides* (at right), towering beside Taiwan cypress (*Chamaecyparis formosensis,* at left).

The botanist Ryozo Kanehira accompanied Wilson in Taiwan. On January 31, 1918, Wilson photographed Kanehira near Mount Arisan, standing beside the trunk of *Taiwania cryptomerioides,* which soared to a height of 150 feet (46 meters).

Clockwise from upper left: *Lithocarpus amygdalifolius* on February 1, 1918; Taiwan Douglas-fir (*Pseudotsuga sinensis* var. *wilsoniana*) on April 6; Taiwan cypress (*Chamaecyparis formosensis*) with a trunk diameter of 20 feet (6 meters), photographed on the return trip, October 31; and *Calocedrus formosana* on April 1.

Wilson photographed pure stands of Taiwan fir (*Abies kawakamii*) on Mount Kiraishu, Nantou County, on March 6, 1918.

nearly 200 ft. tall & 65 ft. in girth of trunk.... I was informed that the oldest tree which had been felled showed about two thousand seven hundred annual rings, & a larger one standing is estimated at three thousand years. The trunks are mostly hollow but the wood, which is reddish, fragrant, & has a beautiful satiny luster, is much esteemed by Japanese for interior work in houses.

FEBRUARY 28, 1918 | TAIPEH, FORMOSA

I returned from the trip to the south on the night of February 26th. The flora of the coastal region did not prove at all interesting, indeed, most of it had been destroyed to make way for sugar, rice, & other crops. However, I made a fair collection of plants & took a dozen photographs so we shall have a record of what the flora is like.

MARCH 16, 1918 | TAIPEH, FORMOSA

The trip to the central range of Formosa has proved a complete success. The weather was fine throughout & the journey fairly easy. From the railway we travelled for two days on push trolley & then climbed for three days, sleeping in police huts at night.... The peak we ascended is named Mt. Kiraishu, is 11,002 ft. high, well-forested on the upper-middle slopes. The climate is drier & the flora different from that of the Arisan region. *Abies kawakamii* [an endemic fir] was the particular quest of the trip & we found it in great plenty above 9,500 ft. After collecting from the ground scales & spikes of disintegrated cones, I was fortunate enough to find four or five perfect cones & so complete the specimens. With this acquisition our herbarium possesses ample & complete material of every known species of *Abies* found in the Far East.… Altogether the trip yielded about two hundred species bringing the total to date collected in Formosa to about four hundred & seventy species. It was difficult country to photograph in but I secured two & one half dozen, which will give a fair idea of the vegetation.

APRIL 11, 1918 | TAIPEH, FORMOSA

I am writing this at the completion of the allotted task in Formosa. One objective I had in mind on visiting the island was to see if possible every conifer known to grow there. Dr. Hayata in Tokyo assured me this was impossible but the local authorities took a more favorable view & thanks to their good services complete success has crowned our efforts. I have seen, photographed, & collected ample material of every species & variety of conifer known from Formosa. But it must be confessed that some of these Formosan conifers have exacted severe toll in time, money & energy & at the moment of writing I am leg weary & tired.… When last I wrote I mentioned that my next trip had for its principal object *Cunninghamia konishii* [another member of the cypress family]. Bad weather hampered things but I got him & photographs also. I then switched off to another district & got the *Libocedrus* [an endemic incense cedar, now recognized as *Calocedrus formosana*] which now is found only on steep ridges & cliffs almost inaccessible. So difficult is the country that it was not possible to obtain photographs of the whole tree but only sections.…

I was back here on April 4th & left the next morning to collect the last remaining species—the Formosan *Pseudotsuga* [an endemic Douglas fir, now recognized as *P. sinensis* var. *wilsoniana*].… On the morning of the fourth day we found our tree but all our efforts to find more failed. Dense fog came on & photography was out of question. The tree was a large one, fully 90 ft. tall & 12 ft. in girth of trunk which divided into three stems.… We then descended some five miles to our lodgings—a police hut—hoping that the next morning would be clear so that we might return & photograph the tree. It rained during the night but morning broke gloriously fine & we got back to the tree by 9 a.m. It stood badly for photography & we were nearly three hours cutting (or rather hacking for our tools were poor) away surrounding trees before a satisfactory picture could be taken. However, fortune favored us but scarcely had we finished when down came the mists blotting out everything. The task accomplished we packed up & returned by the way we came.

APRIL 14, 1918 | TAIPEH, FORMOSA

Formosa is a land wherein it is quite impossible to travel off the beaten track without official sanction & assistance. To us everything has been open & every wish, expressed or implied, viewed favorably. The director of the forestry experimental station, Mr. R. Kanehira, is a very exceptional man full of energy, enthusiasm & good will, & associated with him are at least two very competent collectors. Kanehira arranged all our trips & accompanied us on most of them. We got to know (he speaks English perfectly) one another pretty well & I hope to our mutual advantage. In fact, whilst the tangible results of our trip are considerable no less important in my opinion is the relationship I have established between the Arnold Arboretum & Kanehira & his associates.… Formosa is certainly a rich & beautiful island & its forest wealth is very great. To have visited the island is a privilege I greatly appreciate & I shall carry away with me none but the pleasantest of recollections.

With cordial regards & best wishes,

I am, dear Professor Sargent,

Faithfully & sincerely yours,

E. H. Wilson

DAMERY, J. 2019. HURRIED JOURNEY: BOTANY BY RAIL. *ARNOLDIA*, 76(3): 34–39

Hurried Journey: Botany by Rail

Jonathan Damery

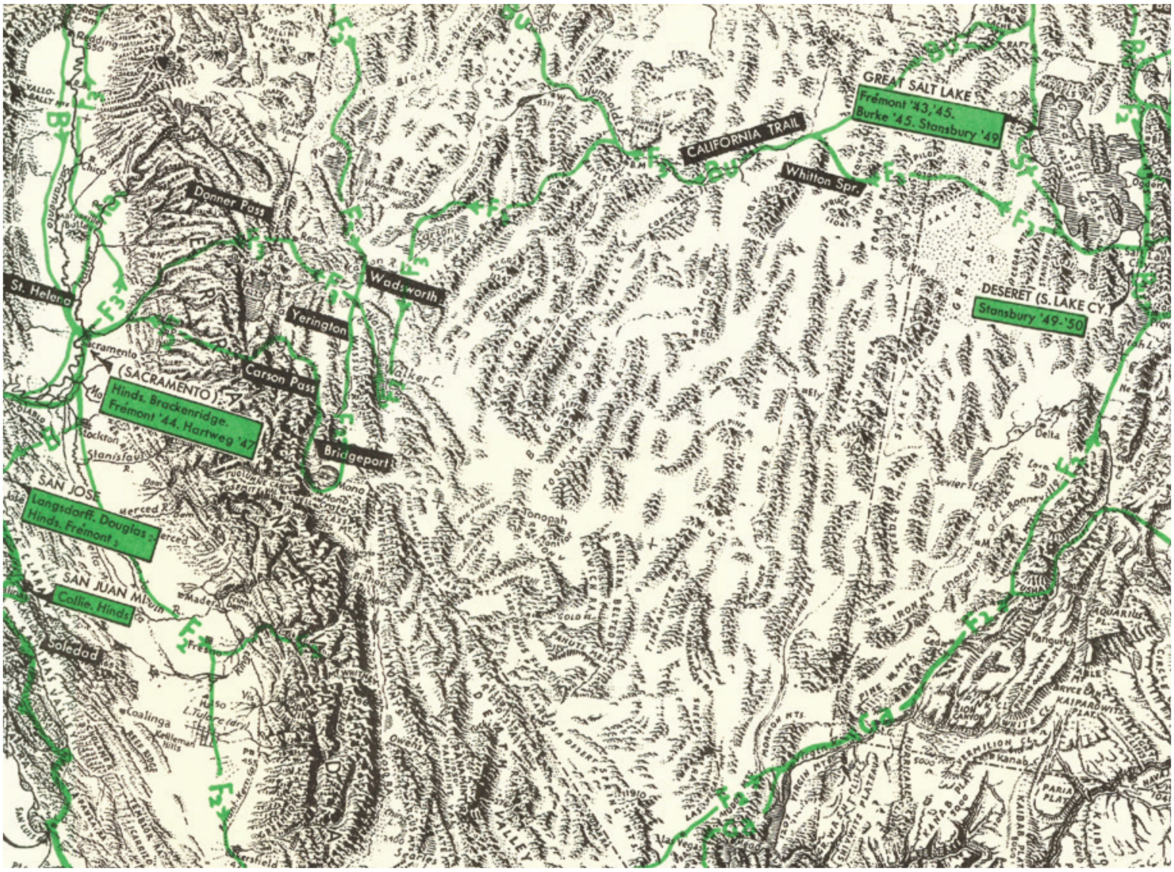
If a pin were dropped in the center of a topographic map of Nevada, it would land amidst a series of low mountain ranges, running roughly north and south. The ranges ripple towards the eastern border of the state, forming an arrangement that looks like a furrowed brow. In 1878, Charles Sprague Sargent, the first director of the Arnold Arboretum, embarked for these arid mountains in what would be the first non-local plant collecting expedition by an Arboretum staff member. Sargent found forests within this area that appeared "scanty and stunted." He counted only seven tree species, of which the single-leaf pinyon (*Pinus monophyla*) and Utah juniper (*Juniperus osteosperma*, then considered *J. californica* var. *utahensis*) were the most abundant. Despite the limited diversity, Sargent was impressed with the trees for their resilience and age. Some, he estimated, were eight hundred years old, if not older.

Sargent began this botanical reconnaissance near the town of Eureka, a silver-mining community located roughly in the center of the state. In 1869, the town consisted of one or two cabins, but by the time Sargent arrived, nine years later, it had grown into the second largest town in the state, with a population, according to boosters, that neared seven thousand. The town boasted a new brick hotel, an opera house that could seat five hundred, two banks, four churches, three newspapers, and, most importantly, sixteen furnaces for smelting silver ore. All of this—along with Sargent's arrival—was facilitated with a narrow-gauge railroad, completed in 1875, which connected Eureka with the town of Palisade, about eighty-five miles to the north. Those tracks, in turn, were made practical by the Pacific Railroad, completed in 1869, which carved its way through Palisade. The Pacific Railroad—composed of the Central Pacific to the west and the Union Pacific to the east—was the first railroad to span the Rocky Mountains and the Great Plains, connecting San Francisco with Omaha and cities beyond.

To Sargent, railroad transportation would have seemed ordinary. After all, his father, a banking president named Ignatius Sargent, had been on the board of directors for several New England railroad companies since 1849, and in 1880, Charles would assume his father's membership on one of these boards—the Boston and Albany Railroad—and would continue in that capacity through 1900. Railroads were in the family. Yet when Sargent headed for Nevada, the Pacific Railroad was less than a decade old, and the railroad was just beginning to redefine botanical possibilities in the western United States. Sargent, himself, described his expedition as a "hurried journey," suggesting how remote landscapes had been rendered newly accessible. Unlike botanical explorations that occurred in Nevada before the ceremonial golden spike was driven on May 10, 1869—the date when transcontinental rail passage was inaugurated—Sargent's field research could be conducted in the matter of two weeks (rather than months or years), with the subsequent research publication written in the comfort of Boston and Brookline.

By Horse and by Foot

In 1955, Susan Delano McKelvey, an Arboretum botanist, published an eleven-hundred-page tome on early botany of the western United States, titled *Botanical Exploration of the Trans-Mississippi West: 1790–1850.* According to McKelvey, an Englishman named Joseph Burke was one of the first scientifically trained botanist to make observations in central Nevada. Burke spent thirty-eight months in the western United States, beginning in the spring of 1844, and he crossed Nevada in the summer of 1846. His account of the Nevada landscape provides scant details, however, because when that portion of the expedition ended at Fort Walla Walla, in southern Washington, he received two overdue letters from William Jackson Hooker, the director of the Royal



ARNOLD ARBORETUM ARCHIVES

A map from Susan Delano McKelvey's *Botanical Exploration of the Trans-Mississippi West: 1790–1850* shows the basin-and-range topography of central Nevada. The botanist Joseph Burke (Bu) passed through Nevada in 1846, partially sharing a route used by John Charles Frémont (F_3) in 1845.

Botanic Gardens, Kew, who was the primary sponsor for the trip. The second letter informed Burke that his funding had been halted due to Hooker's dissatisfaction with the amount of collections Burke had provided. Burke defended his record in a long response letter, noting several shipments of seed—the most recent of which had been sent "across the mountains by the express" and herbarium specimens that had been sent for a ship in Vancouver. Burke then resigned from the expedition. "I think, Sir William, it is a very hard case if a collector is sent from the Royal Botanic Gardens to a country where he cannot send his collections by any means by the time mentioned in your letters," he wrote. "I trust, Sir William, you will forgive my retiring from the service without waiting an answer, as it would be two years or upwards before I could receive one." It would, in fact, take fourteen months for his letter to arrive on Hooker's desk. So, Burke's estimate was realistic, and without the guarantee of money and supplies in the meantime, his explorations could not continue. He returned home.

McKelvey, for her part, felt that Hooker was unfair to Burke, noting the physical rigor associated with backcountry botanical expeditions, where botanists were responsible for travelling with packages of seeds and herbarium specimens—not to mention food and supplies—for weeks if not months on end. "To work one's way thus encumbered through a pathless wilderness of swamps, undergrowth or fallen timber, up and down ravines, across creeks and rivers, in fair weather or in, veritably, foul or to traverse for days on end waterless deserts in horrible heat and permeating dust, was exhausting work, and the collector was not chosen because he was qualified as a Paul Bunyan," McKelvey writes. She goes on to narrate the evening routine botanists were generally obligated to undertake: stopping for camp, building a fire to prepare food and stay warm (even in the desert), and then arranging the daily collections of plant clippings between layers of paper and pressing them tight. Often, too, given that the papers used for herbarium specimens were prone to become damp or wet throughout the course of a trip, the botanist would need to regularly redo older specimens, transferring them to drier papers, in order to prevent mildew. Plant collecting was (and still is) physically demanding.

These routines would have certainly applied to Burke, although it is unclear how many botanical collections Burke made in Nevada. He travelled across the state with a group of settlers that were following a newly blazed trail for Oregon's Willamette Valley. The team consisted of twenty-four individuals and several wagons, and it took nearly seven weeks for them to pass between Fort Hall, on the Oregon Trail, and the Willamette. Burke wrote little about Nevada, but he noted that when the team passed through the northwestern corner of the state, a landscape now known as the Black Rock Desert, it was the "most miserable volcanic region, with many boiling springs." He recorded nothing of botanical interest until spotting an expanse of California poppy (*Eschscholzia californica*), which decorated a recently burned river valley with papery orange flowers, in southwestern Oregon. The poppy was "a very shy fruiter," he wrote, as was the golden chinquapin (*Castanopsis chrysophylla*) that he encountered several days later. When they arrived at the Willamette farmstead where the leader of the wagon train lived, the whole team heaved with exhaustion, horses and humans alike. Burke rested three days and then continued to Oregon City—south of Portland. His horses "nearly drowned" while swimming a creek on the way (presumably soaking any herbarium specimens that he had collected), and it would take him another two weeks to reach Fort Walla Walla, where his resignation letter was ultimately penned.

Over the three decades that separated Burke from Sargent, other botanists passed through northern and central Nevada, and the most detailed observations were rendered by Sereno Watson, who would later become the curator of the Gray Herbarium and Library at Harvard. Watson embarked, in 1868 and 1869, as the lead botanist on two of six field seasons by a geological team surveying the fortieth parallel between California and the Great Plains. Watson's first season focused primarily on central Nevada, the second on Utah—almost entirely within the self-contained watershed of the Great Basin. The region was of interest for the survey (which had begun in 1867) because no accurate maps existed and because the federal government was intent on cataloguing the natural resources along the projected path of the Pacific Railroad.

Watson began at Carson City, Nevada, in April 1868, moving east on an indirect path. The purpose of the survey was thoroughness rather than speed, and the team spent a full six weeks working from a basecamp at Fort Ruby, about seventy miles northeast of the prospecting encampment at Eureka (of which Watson makes no mention). From Fort Ruby, explorations were made in the surrounding mountain ranges and valleys. Watson observed several locations where relatively sizeable conifers could be found, including limber pine (*Pinus flexilis*), growing in the East Humboldt Mountains, with individuals sometimes (though rarely) reaching fifty feet high.

Although Watson documented his findings in incredible detail, he wrote little about the comforts or difficulties of travelling with the survey team, and he said nothing about the logistics of offloading herbarium specimens for shipment. Nevertheless, had his months in Nevada occurred even one year later, the realities of the railroad would have begun to reshape these considerations. By 1868, railroad workers had already begun to lay tracks across Nevada, and in 1869, these tracks were operational. Therefore, Watson's study marked an important moment: not only had it resulted in the most detailed account of the flora of central Nevada published to date but it also represented the final botanical study in the region before the landscape was bound into the national infrastructure of steel tracks and steam locomotion. Geologists on the survey would subsequently comment about strata and fossils observed at railroad cuts, indicating how the presence of the railroad became ingrained in the researchers' world.

Botanical Space

Given that Watson and Sargent would become Harvard colleagues, the men must have conferred about the flora and landscape of central Nevada while Sargent was making travel preparation in 1878. Yet Sargent also saw his trip as a follow-up to an expedition the previous summer by Asa Gray—the preeminent Harvard botanist—and Joseph Dalton Hooker, the English botanist who had assumed his father's role as director of the Royal Botanic Gardens, Kew. When Sargent returned from his trip, he sent Hooker a letter recounting his findings in detail, noting that he expected Hooker would remember the Palisade station on the railroad. Sargent continued south to Eureka, whereas Hooker and Gray continued riding the Pacific Railroad to Carson City. Yet the implications of Hooker's presence in this region is significant, given that thirty-one years before, Joseph Burke was passing through this exact same stretch—then remote and without a defined wagon route—under the direction of Hooker's father. The son, acting in the same official capacity as director of Kew, was making a passage that his father had commissioned another to make.

McKelvey stresses the power dynamics that were often at play between collectors and the individuals who sponsored their trips. She notes that few of the botanists considered in her book—individuals working in the western United States before 1850—were engaging in their own independent research. "By far the greater number went at the behest of professional botanists living in proximity to the essentials of herbaria and libraries, and in distinction to their emissaries, amid safe and comfortable surroundings," McKelvey writes. "The backers of the scheme—often called 'closet botanists' for the reason that, working in offices, they may never have seen the living plants which they described—were engaged for the most part in descriptive botany, writing botanical papers or compiling floras of small or large scope." While Joseph Hooker began his early career with an expedition to Antarctica (and the surrounding islands) and then another to India, those two expeditions collectively required more than seven years abroad. The fact, therefore, that Hooker could now spend scarcely three months travelling from the Atlantic Coast to the Pacific Coast of the United States and back was a radical convenience. Instead of sending an explorer with youthful enthusiasm and resilience—someone like Burke—Hooker himself could go, even as a sixty-year-old and even as the director of a major botanical institution.

For Gray, this was a second trip on the Pacific Railroad; the first was in 1872. Gray's wife, Jane Loring Gray, accompanied him on both trips, and she would later recall him racing into the landscape at short station stops, collecting whatever he could find. This caused considerable intrigue for fellow passengers, who then gathered around to watch Gray prepare his herbarium specimens. Eventually others began to collect plants as well, bringing them to Gray for identification and causing exasperation for the conductor. It took them a day to cross Nevada, where Gray noted the snaking green vegetation along the Humboldt River. In a letter to his friend Richard William Church, Gray described the whole experience with exceptional enthusiasm. "There were fatigues and small discomforts, of course, but these are all forgotten long ago, and the whole transit dwells in memory as one continual and delightful piece of pleasant, novel, ever-varied, and instructive sightseeing," he wrote. "Of course, the identifying at sight, as we flew by, of flowers new to me in the living state, and the snatching at halts, and the physical features of districts which I had always been interested in, and knew much about but had never seen, all gave me occupation and continual pleasure."

In this way, the Pacific Railroad was beginning to reshape botanical space in the western United States. By the time the Grays made their rail passage in 1872, five hundred miles through the Great Basin no longer meant the same thing that it had with Watson's expedition a mere four years before, let alone more than two decades before with Burke. While botanical explorations in the region could still be physical and immersive, the work was conducted with two steel lifelines to urban centers. Herbarium specimens no longer needed to be transported for weeks or months before reaching a shipping location. While Sargent and other leading botanists would continue to enlist field collectors to work in the western United States, the power and money associated with collecting along these railroad axes had been forever transformed.

Botanical Limits

Certainly, the Pacific Railroad did not uniformly influence botanical space in the western United States, and in summer of 1883, Sargent would participate in a geological survey associated with the installation of the Northern Pacific Railroad that connected Tacoma, Washington, with St. Paul, Minnesota. Although he was gone less than two months, that expedition was rife with peril, including two instances where pack animals slipped and fell precipitously. (In the second case, the horse fell fifteen hundred feet, carrying Sargent's plant collections and the team's guns.) Yet Sargent, like others, quickly understood that it wasn't just botanists that would be benefit from this reconfiguration of space along the railroads. The power to study these landscapes came with the simultaneous power to exploit the resources found therein. Both processes could be conducted at an unprecedented rate.

In 1878, after Sargent arrived in Eureka, he obtained a wagon and continued southwest for about seventy-five miles, exploring the Monitor Range, which reaches points well over ten thousand feet above sea level. He then continued to Carson City, from which he proceeded into California. During his two weeks in Nevada, he collected a considerable amount of seed, which he planned to introduce into garden cultivation. Meanwhile, he became increasingly attuned to the risks facing these unassuming and hardscrabble forests. Wood of the Utah juniper (*Juniperus osteosperma*) was widely harvested for cheap fuel, given that it was the only tree

COURTESY OF THE ARCHIVES OF THE GRAY HERBARIUM

Harvard botanist Asa Gray rests at La Veta Pass, Colorado, holding an herbarium press (foreground), with Kew's Joseph Hooker at his side (seated at left). Jane Loring Gray wears a light-colored coat at the table behind. This 1877 expedition continued to California using the Pacific Railroad.

found abundantly at lower elevations. (Its wood even powered the steam locomotive on the Eureka and Palisade Railroad.) Other tree species were harvested for lumber, charcoal, and even bearings for machinery.

Most striking, however, were his observations of the Great Basin bristlecone pine (*Pinus longaeva,* then considered *P. balfouriana*). He found several specimens, growing between fifteen and thirty feet tall, on a mountain near Eureka. "Formerly the whole summit of this mountain was very generally covered with this species," he wrote, "but with few exceptions the trees have all been cut to supply the mines with timbering, for which purpose the strong and very close-grained, tough wood of this species is preferred to that of any other Nevada tree." Sargent didn't estimate the age of these trees or count the tightly packed growth rings, but in California, this species is now known to reach more than five thousand years old. On the same mountain, Sargent observed a curl-leaf mountain mahogany (*Cercocarpus ledifolius*)—a small tree in the rose family (Rosaceae)—and he suggested that plant was least 890 years old, if not much older. "It is perhaps permissible to suppose that the seed which produced this little tree had already germinated when the oldest living *Sequoia* on the continent was still a vigorous sapling with its bi-centennial anniversary still before it," Sargent wrote.

Sargent suspected that someone travelling across the Great Basin on the Pacific Railroad would perceive a landscape that was essentially "destitute of trees," much like the prairies to the east. Yet he came to recognize the "immense value" of the forests, no matter how diminutive. "It will have been seen that the forests of Nevada, consisting of a few species adapted to struggle with adverse conditions of soil and climate, are of immense age, and that the dwarfed and scattered individuals which compose them reach maturity only after centuries of exceedingly slow growth," he wrote. "On this account, and because, if once destroyed, the want of moisture will forever prevent their restoration, either naturally or by the hand of man, public attention should be turned to the importance of preserving, before it is too late, some portions of these forests." He proposed that the federal government should step in to preserve the remaining woodlands, warning that "terrible destruction" would occur otherwise. (About three decades later, the Humbolt-Toiyabe National Forest was established, protecting vast swaths of these noncontiguous mountain forests.) In this sense, Sargent's railroad-powered expedition allowed him to articulate the finite limits of botanical space. Forests that were once remote and practically inaccessible for a Bostonian like Sargent were now mere days away, and their future, as a result, seemed ever more precarious.

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Jonathan Damery is the associate editor of *Arnoldia.*

RUBINSTEIN, J. 2019. SAX PINE: A HYBRID LEFT BEHIND. *ARNOLDIA,* 76(3): 40

Sax Pine: A Hybrid Left Behind

Jared Rubinstein

Last fall, gray fog streamed down the hillside by the Hunnewell Building, enveloping the magnolias and eastern white pines (*Pinus strobus*) that dominate the area. The display emanated from an art installation, Fog x FLO, by Fujiko Nakaya, and when viewing the fog from atop the hill, as signs encouraged visitors to do, a few pines stuck out from the others. With bluish needles and scaly bark, these trees didn't look quite like their neighbors, nor did they look quite like any other species of pine.

That's because these trees (accession 266-46) are hybrids. Although the Arnold Arboretum is best known for its wild-collected plants, most identified to a single species, we also have a significant collection of hybrid plants, including many that were bred and developed here. Karl Sax, a professor of botany at the Bussey Institute and later director of the Arboretum, created some of the Arboretum's best-known hybrids, including *Forsythia* 'Meadowlark' and *Magnolia* × *loebneri* 'Merrill', which both can be found growing in the Arboretum and around the world. But Sax didn't only work with flowering trees or shrubs—he also dabbled with conifers.

In the early 1940s, Karl Sax went on a bit of a pine hybridization kick. Crossing different plant species can be tedious: Pines are wind pollinated, so Sax covered the female cones of one pine species with a bag to prevent natural pollination from pollen blowing around in the wind. When the time was right, he removed the bags and introduced pollen collected from male cones of a different pine species to the female cones. Once the hybrid seeds had developed within the cone, Sax removed and planted the seeds in the nursery at the Bussey Institute. Sax mixed and matched pines from all over the world—New England pines with Himalayan pines, European pines with Japanese pines, West Coast pines with East Coast pines—all with an eye towards producing something new with a high economic or ornamental value.

The hybrid pines behind the Hunnewell Building are crosses between *Pinus monticola,* the western white pine, and *P. parviflora* var. *himekomatsu,* the southern variety of the Japanese white pine. The combination shows just how well hybridization can capture traits from each parent. The needles, in fascicles of five, maintain the long, soft appearance of *P. monticola* but gain a glaucous, blueish-gray color from *P. parviflora.* The hybrids seem to get their height from *P. monticola,* especially accession 266-46*B, which soars to almost 75 feet (23 meters), already much higher than even the oldest Japanese white pines at the Arboretum. And the bark, normally thin and smooth on *P. parviflora* and rough and flaky on *P. monticola,* forms elegant plates that are divided into scales—a sort of middle ground between the two parents.

When evaluating hybrids, one usually looks for hybrid vigor, or traits that give a hybrid an advantage over its parents, like a better form or a higher tolerance to adverse environmental conditions. While these particular hybrids do appear to be vigorous growers and have an unusual mix of features, they never managed to achieve the fame found by some of Sax's other hybrids, like *Prunus* 'Hally Jolivette' or *Malus* 'Mary Potter'. The beauty of these hybrid pines is perhaps a more subtle one, and they just weren't flashy enough to make it big in the horticultural industry of the 1940s. Unlike other pine hybrids Sax tried out, such as *Pinus* × *hunnewellii* or *Pinus* × *schwerinii,* these hybrids were never given a nothospecies designation—that is, a Latin name specific to that hybrid. What's more, these hybrids do not appear in horticultural catalogs or seem common in other arboreta.

Far from diminishing their value, however, this lack of fame makes these hybrids all the more special to the Arboretum. It's possible that the five plants growing here are the sole representatives of this hybrid in cultivation. More than anything, these hybrids highlight the importance of experimentation and of following curiosity to wherever it may lead. Their longevity and beauty remind us that even hybrids that don't "make it" deserve another look.

Jared Rubinstein is the living collections fellow at the Arnold Arboretum.

The ARNOLD ARBORETUM of HARVARD UNIVERSITY