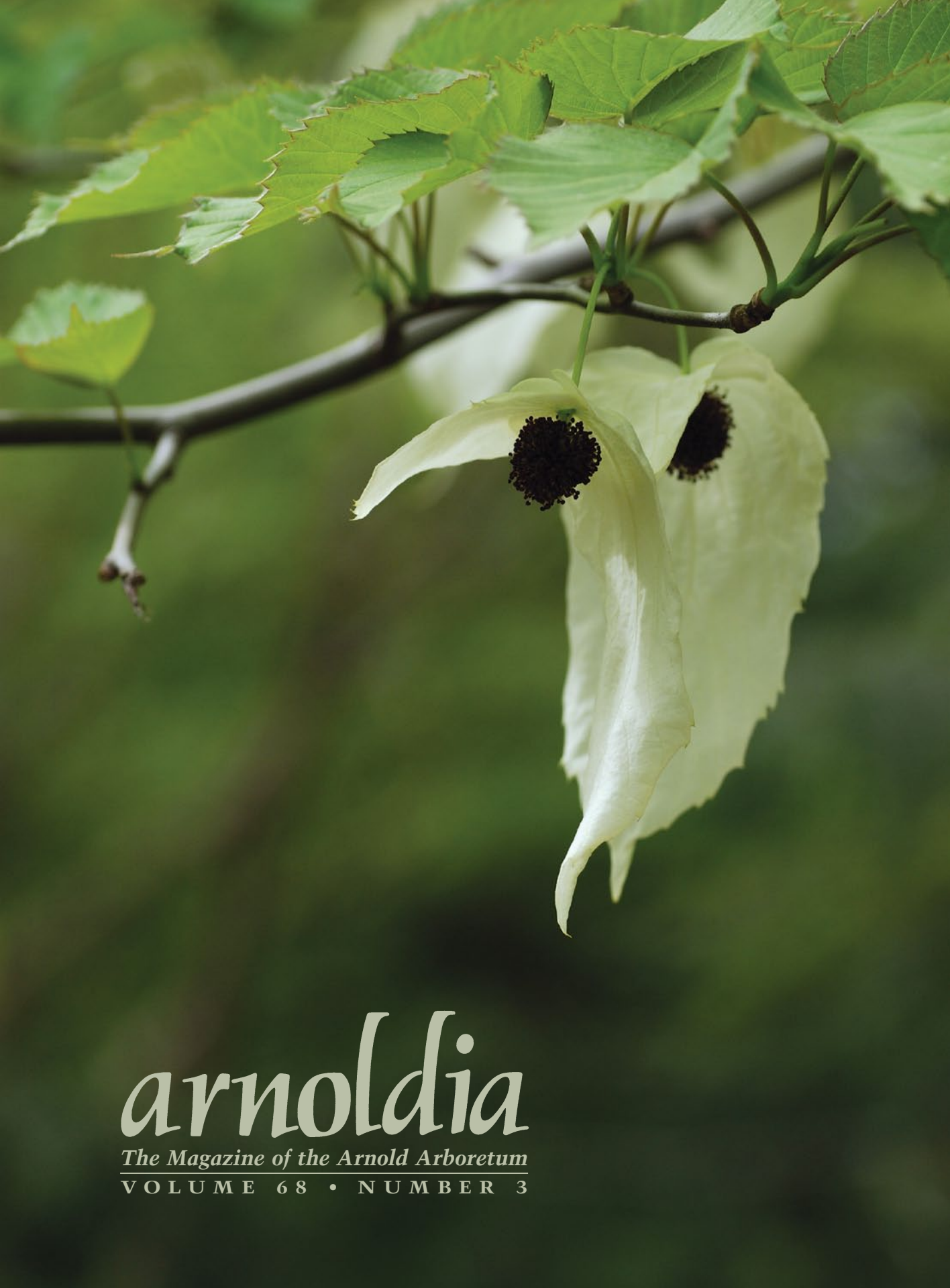

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Inside back cover: Curatorial Fellow Jonathan Damery profiles flatspine prickly ash (*Zanthoxylum simulans*), a tree with both ornamental and culinary appeal. Photo by Nancy Rose.

Back cover: The Arboretum's oak (*Quercus*) collection in winter. Photo by Jon Hetman.

ERRATUM in *Arnoldia* 68/2: The *Castanea* specimen seen in images on page 62 was incorrectly identified as *Castanea henryi.* It appears to be a *Castanea* hybrid; further research is underway to determine its exact parentage.

White Bracts of the Dove Tree (*Davidia involucrata*): Umbrella and Pollinator Lure?

Ji-Fan Sun and Shuang-Quan Huang

Pollen movement in flowering plants depends on various vectors including animals, wind, and water. Compared to wind- or water-pollinated flowers, animal-pollinated flowers are generally showier, often with bright colors. They also often produce nectar or other rewards to attract pollinators. However, the advertisement and reward for pollinators may also attract plant enemies. Herbivores can consume parts of flower structures, entire flowers, or whole plants. For example, nectar robbers may penetrate a hole in the corolla and thereby suck nectar from flowers without playing a pollination role.

The great diversity found in angiosperm flowers can be fully understood only when the diverse floral traits are considered as functional units, shaped by partly opposing selective pressures (Faegri and van der Pijl 1979; Waser and Ollerton 2006). In experimental work on the evolution of floral traits, most attention has centered on natural selection that favors mutualistic pollinators and hinders antagonistic herbivores (Fenster et al. 2004; Strauss and Whittall 2006).

JI-FAN SUN AND SHUANG-QUAN HUANG

A dove tree in bloom at the study site in Shennongjia Nature Reserve, Hubei, China.

A Closer Look at Dove Tree

The dove tree, *Davidia involucrata*, is a species prized by gardeners for its showy bracts. The only species in the genus, dove tree is a medium-sized tree (up to 20 meters [65 feet] tall) that is endemic in mountain forests at altitudes of 1,100 to 2,600 meters (3,600 to 8,500 feet) in western China (Fang and Chang 1983). Fossils from the Paleocene of North America indicate that the lineage was more widespread in the past (for a review, see Manchester 2003).

The genus *Davidia* is named after Father Armand David (1826–1900), a French missionary and keen naturalist who lived in China from 1862 to 1874 and collected many specimens of

PAUL MEYER

PETER DEL TREDICI

Dove trees now grow in gardens around the world, including these specimens at the Morris Arboretum in Philadelphia, Pennsylvania (left), and the VanDusen Botanical Garden in Vancouver, British Columbia (right).

plants previously unknown in the West (Zhang and Li 1994). David was also the first westerner to describe another rare Chinese endemic, the giant panda (*Ailuropoda melanoleuca*).

The dove tree has been considered a first-class endangered plant in China, but it became well-known in its homeland only after it was seen growing in other countries during two diplomatic visits by Chinese leaders. When Enlai Zhou (1898–1976), the first premier of the People's Republic of China, visited Geneva, Switzerland, in 1954, he was impressed by the beauty of flowering dove trees in the gardens of many local families and was told that the tree came from China. Another surprise happened when Chinese leaders visiting Washington, D.C., saw dove trees in bloom in front of the White House in the early 1970s.

The tree's common names—dove tree or handkerchief tree—refer to the two white, paperlike bracts that surround the base of each flower head (capitulum). The bracts initially are small and green, resembling leaves, but increase in size and turn white as the flowers mature. The change in bract color from green to white is associated with the bracts becoming UV (ultraviolet)-light-absorbing (Burr and Barthlott 1993). The anthers are even more strongly UV-light-absorbing. This trait is associated with attracting pollinating insects that see UV light, and the species has therefore been classified as entomophilous (insect pollinated) (Burr and Barthlott 1993), although the pollination of *Davidia involucrata* had not been previously studied in the field. We are particularly interested in the questions "What is the function of the white bracts? Do the dove tree's bracts play a role in attracting pollinators?"

Many plants within Cornales, the dogwood clade, have large bracts that surround the inflo-

COURTESY OF KEVIN NIXON

The colorful bracts surrounding the small flowers of this *Dalechampia* attract pollinators.

rescences. Bracts have been thought to protect flowers from herbivores in various species. For example, the bracts of *Dalechampia* vines function as honest signals to pollinators of the presence of floral reward (Armbruster et al. 2005) and also function in protection from florivores (flower eaters) and pollen thieves (Armbruster 1997).

Flowers are also under strong selection pressures from their physical environment, yet research on selection by abiotic environmental factors on flowers has been limited (Corbet 1990; Galen 2005). During our previous field work, our observation was often interrupted by rainy days. Rain is one of those abiotic factors that acts as a selective agent on flowers. This was first recognized by Sprengel ([1793]1972), who noted that rain may wash away pollen grains and dilute flower nectar. This added another question to our research: Did the need to protect pollen grains from rain play a role in the evolution of large bracts?

Carrying Out the Study

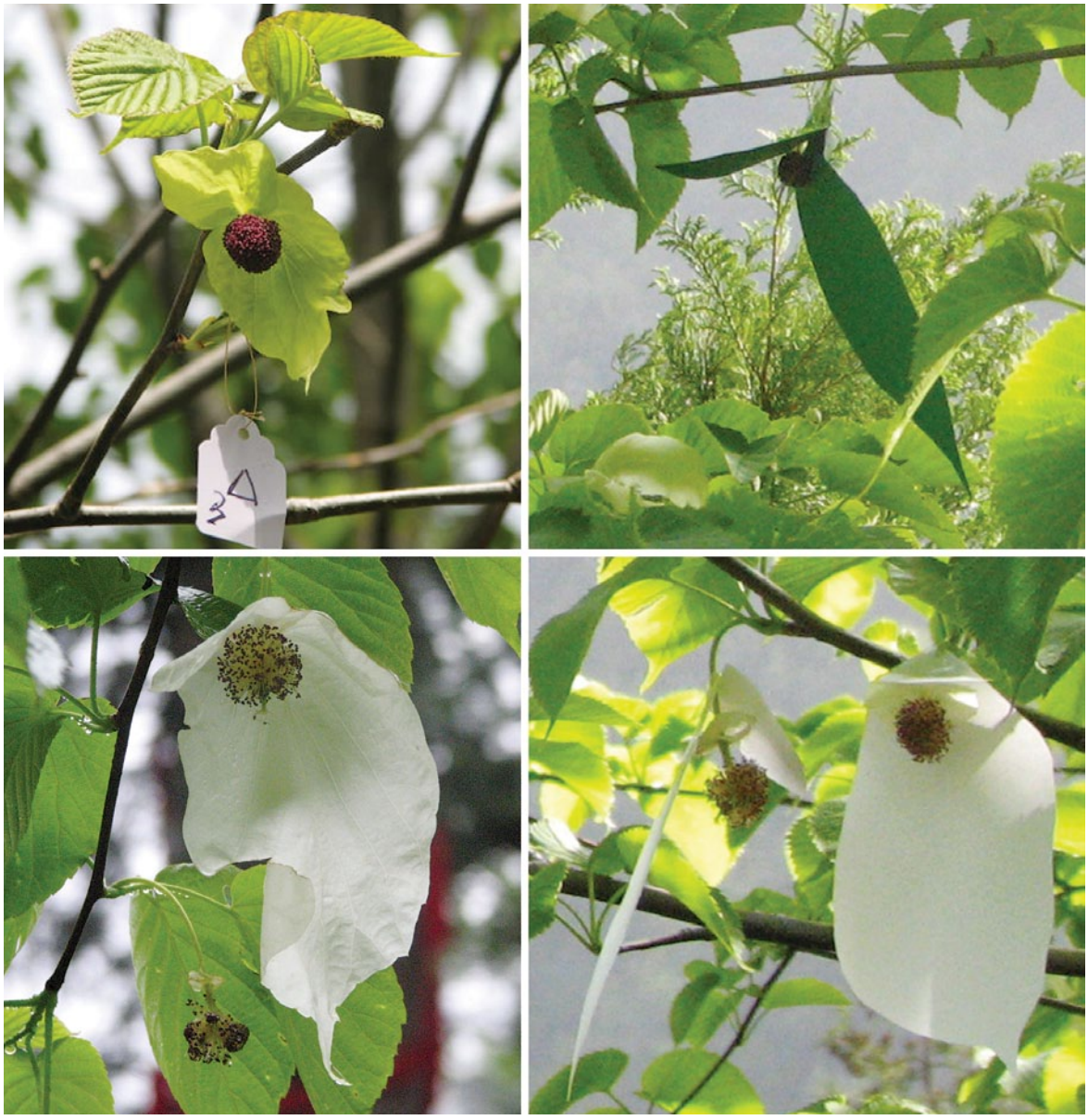
With our questions about rain protection and pollinator attraction in mind, we carried out observations and experiments in a natural population of dove trees in western China (Shennongjia Nature Reserve, Hubei) in April 2005 and April 2006. In our study, we manipulated flowers in a population of 16 flowering dove trees to assess the function of this species' bracts.

Though dove tree's mature bracts draw much attention, the round inflorescences dangling beneath the bracts are also interesting. The dark purple inflorescences generally consist of a single perfect (holding both stamens and pistils) flower surrounded by numerous male flowers (Fang and Chang 1983). The individual flowers are naked and nectarless, without sepals or petals. Before flowering, dove tree's bracts are green, turning white rapidly as flowers mature and anthers begin to dehisce. The anthers split longitudinally, and pollen grains are exposed on the recurved anther walls. Individual capitula of the dove tree last 5 to 7 days and the bracts drop off when flowering ends.

As part of the study, we collected both green and white bracts and preserved them for later observation under the microscope. We also measured the length and width of the bracts on each of 20 capitula daily between April 16 and April 22, 2006.

Do Dove Tree's Bracts Function in the Pollination Process?

To investigate the role of bracts in pollinator attraction, we recorded pollinator visits to four kinds of capitula: (1) natural, (2) with both bracts removed, (3) with both bracts replaced by green artificial bracts made of copy paper, or (4) with both bracts replaced by white artificial bracts made of copy paper. The artificial bracts were similar in shape and size to the natural bracts. We recorded the number of pollinator visits to the dove trees' flowers from 10:00 in the morning to 3:00 in the afternoon between April 18 and April 22 in 2005, and between April 16 and April 20 in 2006. Two observers monitored two sites during these periods of maximum pol-



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Clockwise from upper left:

A young inflorescence displays still-green bracts and deep purple immature anthers.
An artificial inflorescence in which the natural white bracts were replaced with green paper.
Two artificial inflorescences in which the natural white bracts were replaced with white paper.
Two mature inflorescences, the upper one is untouched, while the lower one has had the bracts removed.

linator activity. Insect visits became extremely rare after 3:00 in the afternoon, and during one night of observations, no pollinators were observed visiting this nectarless species. Pollinators were collected and sent to the Institute of Zoology of the Chinese Academy of Science in Beijing for identification.

To examine whether capitula with intact bracts lost more or less pollen to rain than did capitula that had their bracts removed, late in the flowering period we counted the pollen remaining within 29 and 27 capitula that were natural or had both bracts removed, respectively, and had experienced at least one rainy day.

Numbers of anthers and ovules per capitulum and pollen grains produced per anther were estimated in 34 capitula with freshly dehiscing anthers. In September 2005 and 2006, we collected 39 and 32 open-pollinated capitula and counted their seeds to estimate seed set under natural pollination.

Pollen Stickiness and Behavior in Water

The pollen grains of anemophilous (wind pollinated) plants are not sticky, while those of entomophilous plants usually are sticky in order to adhere to visiting pollinators. To assess the possibility of wind pollination of dove tree, we tested the stickiness of its pollen grains by their adherence to glass slides. We also placed netting around 20 capitula, thereby excluding pollinators but allowing possible wind pollination, and later examined the netted capitula for seed production.

To test the behavior of pollen grains under rainy conditions, we followed Huang et al.'s (2002) method of pollen germination. Pollen grains from newly dehisced anthers were placed in sucrose solutions of 5%, 10%, 15%, and 20% by mass to examine optimum conditions for pollen germination. We then compared germination rates of pollen grains from eight randomly collected capitula in distilled water or in the optimum sucrose solution (10%). Pollen grains that had either germinated or burst after 4 hours were counted under a light microscope. Ten samples of pollen grains from each flower were analyzed in this manner. Data analysis was accomplished by using one-way ANOVA analysis to compare the frequencies of pollinator visits to the four kinds of capitula and the amount of pollen remaining in capitula after different experimental treatments and to assess pollen viability in distilled water versus 10% sucrose solution.

What We Found Out…

When we looked at the dove tree bracts that we had collected at either the green or white stage, we saw that the parenchyma cells in the green bracts were full of chloroplasts, while the parenchyma cells of white bracts had degenerated and contained few chloroplasts. Bract color turned from green to white on the third or fourth day, when the anthers began to dehisce and when bracts had reached three-quarters of their final size. Bracts continued to grow during anthesis but dropped off soon thereafter.

Pollen-collecting bees and pollen-feeding beetles were the major visitors and pollinators of the flowers. We recorded a total of 2,174 visits to capitula, of which bees and beetles accounted for 93.6% and 6.4%, respectively. Beetles generally stayed within a capitulum for 1 to 2 hours, while bees spent 4 to 6 seconds per capitulum foraging for pollen, suggesting that bees are the more effective pollinators of the dove tree. Bees that visited included *Apis cerana, Xylocopa appendiculata* (Apidae), and *Halictus* and *Lasioglossum* species (Halictidae), and beetles included *Agriotes* species (Elateridae), *Oxycetonia jucunda* (Cetoniidae), and species of Nitidulidae. Visitor frequencies were low, and so was seed set of open-pollinated capitula in both years. It seems clear that wind pollination of dove tree is unlikely since its

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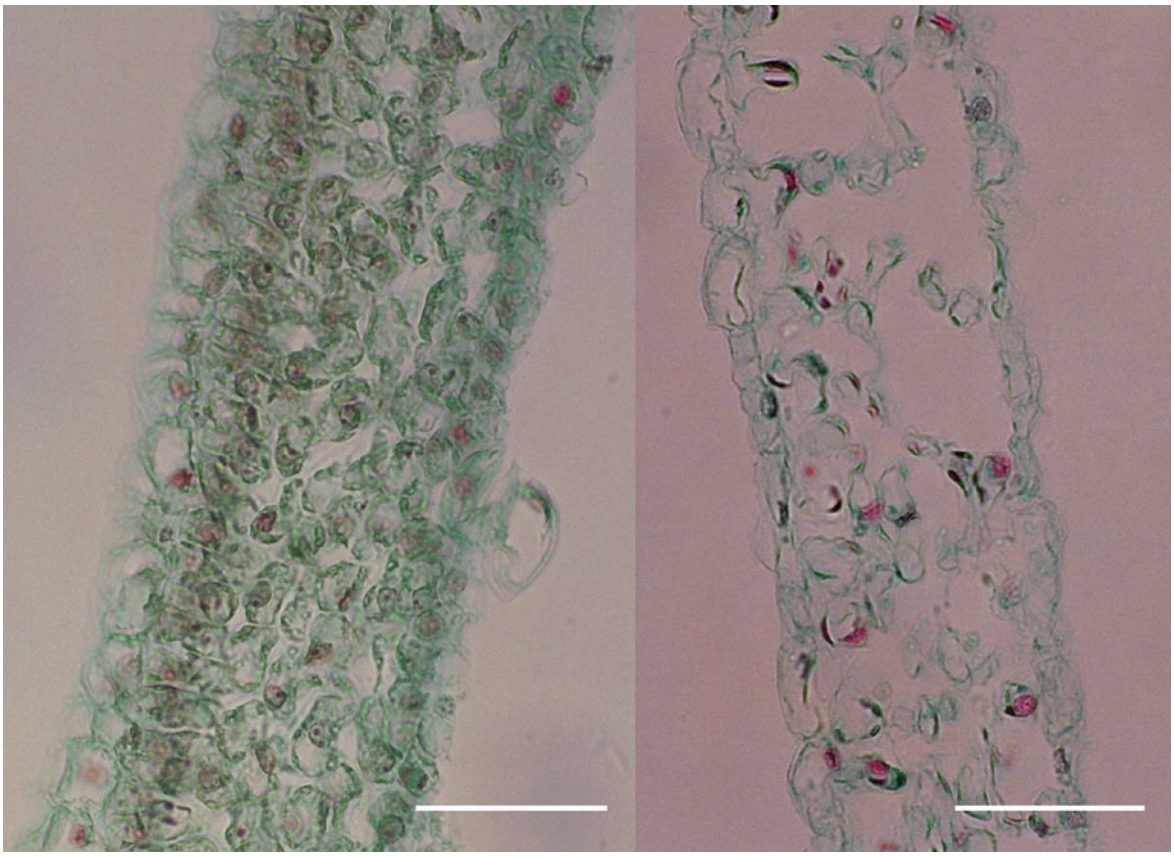
Pollen grains of *Davidia involucrata* germinating in 10% sucrose solution.



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Cross sections of a green bract (left) and a white bract (right). Mesophyll cells and chloroplasts have degenerated in the white bract. Scale bars = 0.5 millimeters (0.02 inch).

pollen grains are sticky and apparently not picked up by wind. Also, the netted capitula did not produce any seeds, further evidence that insects rather than wind pollinate dove tree flowers.

Bees preferred to visit capitula with white bracts over those with green bracts, on the basis of four consecutive days of observations on inflorescences of 62 natural capitula, 62 bractless capitula, 62 white-papered capitula, and 48 green-papered capitula. Visits to natural and white-papered inflorescences were not significantly different but were higher than those in the other two treatments. Visits to inflorescences with bracts removed and those with bracts replaced by green paper did not differ significantly.

The pollen/ovule ratio in *D. involucrata* is extremely high, with a capitulum producing only about 7 ovules to about 900 to 1,000 anthers, which produced over a million pollen grains in total. Pollen amounts remaining in capitula with their bracts removed were not significantly different from those in intact capitula but were significantly lower than the

ZACHARY HUANG, HTTP://BEES.MSU.EDU

The Asian honey bee *(Apis cerana)* was one of the pollinators found on dove tree flowers. The specimen seen here is feeding from Chinese elderberry *(Sambucus chinensis)* growing in Sichuan, China.

total pollen production, demonstrating high pollen loss to rain or removal by pollinators.

Pollen germinated best in 10% sucrose solution, and there was a highly significant difference in germination and bursting rates between pollen grains placed in distilled water or 10% sucrose solution. After 4 hours, about 85% of pollen grains in water had burst, while only about 37% of the grains in 10% sucrose solution had burst. (ed. note: see Sun et al. 2008 for detailed results)

… and What It Means

Pollen-collecting bees, the most important pollinators of *Davidia involucrata*, preferred visiting white-bracted capitula, and it is therefore likely that during their green stage the bracts function in photosynthesis, while during their white, UV-light-absorbing stage their function changes to attracting pollinators. During more than 170 hours of observation, we never observed bees visiting green-bracted capitula. Their UV-light absorbance makes the white bracts stand out from surrounding foliage in the bee visual spectrum (Burr and Barthlott 1993; Kevan et al. 1996) and is likely due to the flavonoids that are the major pigments in the bracts of *D. involucrata* (Hu et al. 2007).

Over the 2 years of our study, insect visitation was low. With low visitation rates, prolonging the flowering period will benefit reproductive success as a sit-and-wait strategy (Ashman and Schoen 1994). Protection of the pollen grains presented on the recurved anther walls during the 5 to 7 day flowering period would then be of key importance; the longer viable pollen is

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Greenish immature bracts function photosynthetically, while mature white bracts absorb UV light and function in attracting pollinators. Note that many of the anthers have already dehisced in the mature inflorescences.

present, the better the chance of a pollinator visiting within that period. Since dove tree's flowers lack a corolla, protection of the pollen must be achieved by the bracts. Dove trees generally flower from mid-April to mid-May, a period which is within the rainy season of the subtropical region where they occur. Since the pollen grains of dove tree readily burst in water, it is probable that the rooflike bracts function as an umbrella to reduce rain damage to the anthers and pollen. Indeed, we repeatedly observed rain-damaged stamens in the capitula where we had removed bracts, while capitula with intact bracts had dry stamens even after heavy rain. The fact that bract-bearing capitula lost as much pollen as bractless ones is attributable to bees removing most pollen from the former, while rain washed away most pollen from the latter.

The evolution of flower or inflorescence structures with multiple functions may reflect the net effect of conflicting or additive selective pressures (Anderson 1976; Armbruster 1996, 1997, 2001; Galen 1999; Fenster et al. 2004; Armbruster et al. 2005; Strauss and Whittall 2006; Waser and Ollerton 2006). In the case of the dove tree, pollinator selection favors white bracts, while the need to protect pollen from rain favors large bracts. Notably, dove tree's two bracts differ in size, perhaps in response to constraints on weight or resources.

Experimental studies of the effects of rain on floral traits are scarce (Bynum and Smith 2001; Huang et al. 2002; Galen 2005). Recent studies of pollen longevity in 80 angiosperms found that pollen life-span was decreased by direct contact with water (Mao and Huang 2009). Another evolutionary tactic is seen in the erect flowers of *Primula vulgaris;* though the flowers regularly fill with water, roughly a quarter of the primula's pollen grains will still germinate even after 5 hours underwater (Eisikowitch and Woodell 1975). While some species have relatively high water-resistant pollen, others rely on nodding flowers, or close their flowers by petal movements (Bynum and Smith 2001; Hase et al. 2006; He et al. 2006), or have other features protecting pollen from wetting, such as in the dove tree.

ROBERT MAYER

The pale green bracts above these *Tilia* (linden) flowers may serve several purposes, including attracting pollinators.

It seems that the bracts of the dove tree are a striking example of the multiple roles played by one structure in photosynthesis, pollinator attraction, and as a stamen rain shelter. As another example, in *Tilia* the bracts not only help wind dispersal of the fruits once they mature, but also may act as flags that attract pollinators— especially nocturnal pollinators— to the flowers (Anderson 1976). Our observation of the multifunctional nature of bracts in the dove tree suggested that floral traits are under selection pressure from mutualists and antagonists as well as selection by abiotic environmental factors.

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Little Big Plant, Box Huckleberry *(Gaylussacia brachycera)*

Rob Nicholson

Box huckleberry's foliage looks somewhat similar to boxwood (*Buxus* spp.), which explains its common name. (PHOTO BY ROB NICHOLSON)

It is one of the charms of the science of botany that the most subtle species can contain the most elegant mysteries. Such is the case with box huckleberry (*Gaylussacia brachycera*), an evergreen subshrub with small, glossy, leathery leaves. Box huckleberry grows in the full shade of mixed pine–oak forests in sporadic locations from Pennsylvania to Tennessee (including a fairly recently discovered site in North Carolina [Wilbur 2004]). While this species has been known to botanists for centuries, it is an example of how knowledge builds on knowledge and how even familiar subjects can still be a source of discovery.

This low-growing shrub is in the Ericaceae (heath family), an assemblage of plants that includes heaths (*Erica*) and heathers (*Calluna*), rhododendrons and azaleas (*Rhododendron*), blueberries and cranberries (*Vaccinium*), and madrones (*Arbutus*). It is a fairly large family with species found throughout much of the world. The huckleberries, along with the blueberries, are grouped in a subfamily called the *Vaccinioideae.* Blueberries (*Vaccinium*) and huckleberries (*Gaylussacia*) are traditionally separated botanically by the number of chambers (called locules) within the fruit and the size of the seeds.

While the name huckleberry may bring forward associations to Mark Twain's all-American rascal, Huckleberry Finn, the genus *Gaylussacia* shows a predominantly South American bent. The center of species diversity for the genus is southeastern Brazil, with 37 species found in the hills and mountains near the Argentine border. A few more species are Andean, but then a separation of 1,100 miles (1,770 kilometers) occurs before reaching any of the North American species, the closest being *Gaylussacia dumosa* in southern Florida. Eight *Gaylussacia* species are known from the eastern United States and Canada, but none have been found in Mexico, Central America, or the Caribbean—a somewhat mysterious gap.

The huckleberries have traditionally been further divided into three subgroups called sections: section *Vitis-idaea,* with only *Gaylussacia brachycera;* section *Decamerium,* with three North American species; and section *Gaylussacia,* with *G. mosieri* of the Florida panhandle and all the South American species. (Some recent research [Floyd 2002] questions whether *Gaylussacia* should be divided into sections at all.) So this odd distribution of species and subgroups presents the first botanical puzzle that heavily involves the little box

huckleberry: on which continent did the huckleberries first evolve, and how did they then spread? And where did this unique species—*Gaylussacia brachycera*—come from?

Have Berries, Will Travel

The migration route traveled by *Gaylussacia* between the southern and northern landmasses is unclear, with one botanist (Camp 1941) postulating a gradual migration over a former landbridge, a connection to the east of the Isthmus of Panama. Another (Floyd 2002) suggests the possibility that the genus originated in North America, rather than South America.

Gaylussacia brachycera is different from all other species within the genus in that it lacks glands upon its leaf surfaces, and is therefore segregated into its own section. Its original discoverer, the French botanist André Michaux, thought it to be a *Vaccinium* and published it as such in 1803. However, it has an ovary split into ten chambers like its brethren *Gaylussacia* rather than the five chambers usually associated with blueberry, and it also has large seeds rather than the tiny seeds typical of blueberries. Anyone who has sampled wild huckleberries knows they have more crunch than blueberries and are probably less developed as a food crop because of this seediness.

I had reason to believe I had found a "missing link" on the path between North and South America while collecting in the high pine forests of northeast Mexico. I came upon a low-growing, thick-leafed plant that I immediately took to be a species of *Gaylussacia* because of its close resemblance to box huckleberry. I was excited by the biogeographic implications, and cuttings were collected and brought back to the botanic garden for propagation. When the resulting plants finally flowered I was able to dissect the flowers and determine the plant's true identity. If it was a blueberry then the ovary of the flower would have five compartments, if a huckleberry, then ten. I focused my microscope on the sectioned ovary and saw a pie of five wedges resolve itself. The plant was determined to be a Mexican species of blueberry, *Vaccinium kunthianum*. It was my ultimate anti-Archimedean moment, the crashing flip side to "Eureka!"

ROB NICHOLSON

***Gaylussacia* seeds (seen here) are larger than those of *Vaccinium*, giving huckleberries a distinct crunchiness when eaten.**

Depending on which taxonomic interpretation one subscribes to, *Gaylussacia brachycera* is a unique species among the huckleberries, or has two very close relatives in southern Brazil. Alternative positions have constantly swirled around box huckleberry; Camp (1941) wrote "it would certainly appear to merit generic rank," while recent molecular genetic studies by Dr. Jennifer Whitehead Floyd (2002) show that the box huckleberry may be intermediate between the huckleberries (*Gaylussacia*) and blueberries (*Vaccinium*) and may be an ancient hybrid involving species from each camp. But if it is a hybrid, what were the parents? And where might the ancestral lines be? Further molecular genetics studies may finally crack the riddle or even return the species to the *Vaccinium* fold, where it started with Monsieur Michaux two hundred years ago.

How Old Is Old?

Gaylussacia brachycera was first found around 1796 by the French botanist André Michaux at Warm Springs, Virginia, a locale now shrouded in confusion. Two other collectors found it in the early 1800s, both in West Virginia. Fifty years would pass before another, more northern stand in Perry County, Pennsylvania, was discovered by Spencer F. Baird, a young professor of natural history at Dickinson College who later went on to be Secretary of the Smithsonian Institution.

***Facing page:* Black huckleberry (*Gaylussacia baccata*) is distributed throughout the eastern United States and eastern Canada. This deciduous *Gaylussacia* species is noted for its bright red autumn foliage.** (PHOTO BY NANCY ROSE)

How Old Are You Now?

THE MEASUREMENT of age in living plants can be done with a limited number of species. Only those ligneous (woody) plants that live in temperate or arctic regions and are exposed to annual weather cycles will dependably create rings that correlate to age. The title holder for oldest plant is still under contention. Among the most vaunted contenders are the Great Basin bristlecone pines (*Pinus longaeva*) of California's White Mountains with tree ring counts of over 4,000. A specimen of the magnificent alerce tree (*Fitzroya cupressoides*) in Chile has recently been shown to have ring counts of over 3,600 years, and some Saharan cypress (*Cupressus dupreziana*) in Algeria are probably over 2,500 years old.

These species all form rings and are arborescent species, having a single trunk. Interesting also, they are all conifers. Tropical trees don't form dependable dating rings, so despite the great size and age that some of these attain, they are bystanders in the contest. Also excluded are those species that aren't trees. Clump forming shrubs or herbaceous perennials, such as azaleas and iris, can persist for many generations and slowly increase their size and number of stems. The limits of age on shrubs are unknown, although some documented plantings in botanic gardens are well into their second century.

In fact, some of the oldest plants may appear as entire forests or large assemblages of individuals. Many poplar (*Populus*) species, including quaking aspen (*P. tremuloides*), can send up multiple individual trunks from a single vast spreading and interconnected root system. These colonies can expand and contract over time depending upon competition, climate, and catastrophic events such as forest fires. Entire mountainsides have been revealed to be covered by a single clonal stand of many trunks connected by a subterranean network of roots. With clonal colonies such as these, estimating age is next to impossible, though in two notable cases this has been attempted. One is the box huckleberry, as described in this article. The other is creosote bush.

The shrub *Larrea tridentata,* known as creosote bush because of its prodigious production of resin, grows in arid regions of the southwestern United States and north central Mexico. Growth of creosote bush colonies begins with the original founding event, the germination of a seedling. As the plant grows, its lower branches come in contact with the soil and develop their own roots. Over time the interior portions of the clump die and a ring of plants, slowly increasing in diameter over time, is formed. In the 1980s, botanist Frank Vasek radiocarbon dated chunks of deadwood at the centers of the oldest and largest rings and derived an average growth rate for creosote bush in his region. By applying this rate to the largest clone (for which he found no wood at its epicenter) a phenomenal figure of 9,400 years was obtained (Vasek 1980). This champion plant is now known as "King Clone" and is protected on a 17-acre preserve.

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Annual growth rings can be seen in the stems of woody plants in temperate or arctic regions. A cut trunk of common alder (*Alnus glutinosa*) is seen here.

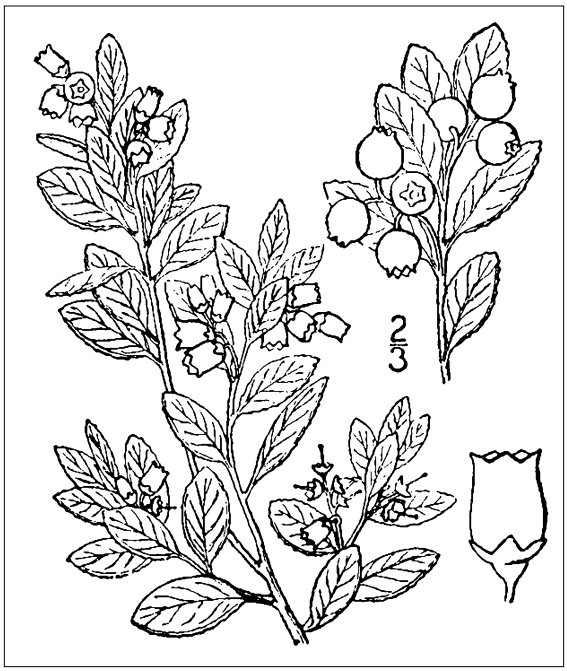
In 1919, the botanist Frederick Coville postulated (on the basis of morphological characteristics and the inability of the plant to set viable seed) that the large 1,200-foot-long (366 meters) stand in Pennsylvania seemed to be a single clone and had spread across the gentle slope by means of underground runners. It was observed that the plant grew laterally about 6 inches (15.2 centimeters) a year so he estimated that the entire clump had incrementally increased to its present size from a single seed deposited 1,200 years prior.

A sister clump, across the Juniata River from the Baird stand, was found in 1920 by H. A. Ward. This was the largest single stand ever to be found, a massive colony stretching over a mile and covering 100 acres (40.5 hectares). Coville's methodology was applied to this monster and an age estimate of 13,000 years was declared.

Based on fossil pollen studies, we now have a clearer picture of what the climate and flora of this area would have been like over 13,000 years ago, and these data alone would probably debunk the age claim. The leading edge of the glacier terminated about 75 miles (120.7 kilometers) to the north of the position of the goliath clump around 18,000 to 20,000 years before the present day. As little as 10,000 years ago central Pennsylvania was covered in a boreal forest association, one that would probably have been too cold for the box huckleberry. The current forest, a mix of conifers and deciduous species, started to come into place about 8,000 years ago.

Box huckleberry covers the forest floor at this Pennsylvania site. (PHOTO BY ROB NICHOLSON)

USDA-NRCS PLANTS DATABASE



Botanical illustration of *Gaylussacia brachycera* from Britton and Brown's *An illustrated flora of the northern United States, Canada, and the British Possessions,* published in 1913.

In the years since Coville's conjecture, the interstate highway system has had more impact on the plant than any glaciers. During the 1960s a large portion of the goliath colony was eradicated by the installation of US Route 22/322, and a forest fire also diminished it. Sadly, this construction predated the stronger environmental standards in place today in Pennsylvania, which require highway contractors to inquire about rare and endangered plants in their paths. The conservation status of box huckleberry varies among the states where it is found, but in Pennsylvania it has a ranking of S1—critically imperiled. The species global conservation status, which considers all populations in total, is G3—vulnerable. The tract of land where the original Baird clump grows is now a Pennsylvania State Park while the remnants of the goliath clump are in private hands. The owner is aware of the plant's legacy and seems proud to direct the botanically inclined to its location.

Box huckleberry's evergreen leaves and delicate bell-shaped flowers are highly ornamental.

A Short Walk Through a Short Giant

I contacted him, got precise directions, and made a weekend pilgrimage to collect research material from this diminished Methuselah. The two Pennsylvania stands of box huckleberry are in the upper end of the ridge and valley system that stretches from Pennsylvania to Alabama. A drive along the interstate brought me to the top of a bedrock fold overlooking the broad and muddy Juniata River. As directed, I turned from the river and walked into the woods. It was a plain piece of land, a common mix with red maple (*Acer rubrum*), hickory (*Carya* spp.), chestnut oak (*Quercus prinus*), white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*) standing tallest, while below these grew shadblow (*Amelanchier* spp.) with highbush and lowbush blueberries (*Vaccinium corymbosum, V.angustifolium*). It would have been quite possible, if you weren't keyed onto it, to walk past the box huckleberry thinking it a variant of lowbush blueberry, or not noticing it at all. Its thick, bright green, leathery leaves are held on wiry pinkish-green stems, and the small, bell-shaped, white and pink flowers are borne in clusters. Its fruit could easily pass for a blueberry, at least until they are chewed, at which point their larger and coarser seeds interrupt the anticipated gastronomic explosion of blueberry deliciousness.

In the filtered shade the box huckleberry grew to a height of 8 inches (20.3 centimeters) and formed a patchy patch, denser in some sections than in others. The outer edge of the colony was amoeba-like, its edge curving in and out through the trees. Nearest to the highway was an area of woods that had recently burned, and here the box huckleberry had leaves of a more anemic green, perhaps sun-scorched from want of a shady canopy. After some concentrated tramping, I found another small patch on the slope of a neighboring ridge and sampled this also over two transects. Along with the Baird stand across the river, this would make a total of three separate Pennsylvania populations in the study.

I had questioned whether genetic analysis could tease apart these stands to determine whether these large clumps were indeed a single individual run amok or were many indi-

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Box huckleberry forms a sprawling carpet of green in shaded woodlands.

viduals that had merely coalesced together. Dr. Margaret Pooler of the United States National Arboretum had begun some genetic analysis of the species and we agreed that this clonal analysis would make an interesting research subject and also help in determining conservation strategies for this rare species.

I established two perpendicular transects across the length and breadth of the clump and then sampled at equal distances along these. I brought cuttings back to the Smith College Botanic Garden, rooted them, and kept them all in separate pots as they grew. The analysis of each sample's genes would show how closely related each of the samples was to one another. If identical in genetic makeup then Coville's single-clone theory would gain credence.

To complete the study, material was also collected from a stand in north central Tennessee. The lovely town of Rugby is a quaint cluster of 20 Victorian homes in the woods, a former utopian community now under siege by antique hounds. A path through the woods leads to the Gentlemen's Swimming Hole, and here, growing with the spectacular mountain stewartia (*Stewartia ovata*), is another outsized patch of box huckleberry, which was also transected and collected for the study. Finally, a sample of the low-growing Mexican *Vaccinium kunthianum* was also sent to the United States National Arboretum for analysis.

Little Plant, Big Data

After the team at the National Arboretum did their genetic analysis they found the Tennessee stand was a single clone and the Mexican material was very distantly related. The Baird stand of Pennsylvania showed only two clones, with one clone limited to one corner of the huge clump. Those from across the river were very different. The smaller of the two showed three closely related clones. But a quarter mile away, the largest clump of all—at nearly 1,000 feet (over 300 meters)—showed but one clone. Using the estimated growth rate of 6 inches (15.2 centimeters) per year, this would make this stand 1,000 years old had it started in the middle but 2,000 years old had it begun at the end. Because of the destruction of 80% of the stand we will never know if the entire mile

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Rooted cutting of *Gaylussacia brachycera.*

length was once all connected and genetically identical. But what was left of Coville's "charming little thousand-year-old lady of the forest" may indeed be the oldest known woody plant east of the Rocky Mountains.

Space and time are key concerns of our human species and we tend to measure other species by our own familiar rulers and clocks. These large clonal plant stands put the lie to the idea that plants do not move or locomote. A plant specimen will cover distance, but in an imperceptible fashion relative to our lifespan and our ways of moving. It just moves to a slower, millennial-scale timepiece rather than the sweeping second hands that so many of us caffeine-addled commuters adhere to. Perhaps we should all aspire to so relaxed a pace.

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General Forest Ecological Processes
Chapter 10 from *Trees and Forests, a Color Guide*

Peter A. Thomas

INTRODUCTION

Wooded land currently covers between 30 and 35% of the world's land surface (depending on what is counted as forest), or around 39 to 45 million k^2 [15 to 17 million square miles] (FAO 2003). Ecologists often distinguish between woodland and forest. Woodland is a small area of trees with an open canopy (usually defined as the canopy giving less than 40% cover, that is 60% or more of the sky is visible) so that plenty of light reaches the ground, encouraging other vegetation beneath the trees. By contrast, a forest is usually considered to be a relatively large area of trees forming a closed, dense canopy. For simplicity's sake, and because the underlying ecological processes at work are the same, in this chapter the term forest will be used to mean any wooded land.

ALL PHOTOS BY THE AUTHOR

A dense temperate rain forest in the Olympic Peninsula, Washington State, USA. It is composed mostly of *Psuedotsuga menziesii* (Douglas fir), *Tsuga heterophylla* (western hemlock), and *Thuja plicata* (western red cedar).

Open woodland at Needwood Forest, England. The sparse canopy of *Fraxinus excelsior* (European ash) and *Tilia* spp. (lime [linden]) standards allows abundant light to reach the shrub layer of coppiced *Corylus avellana* (hazel) and, on the ground, a mixed field layer dominated by *Hyacinthoides non-scripta* (bluebell). A sparse ground layer of mosses is also present.

SIZE AND GROWTH

The most obvious factor that separates forests from other types of habitat is the large weight or mass of organic material present, referred to as the biomass (or sometimes the standing crop). In most forests, more than 85% of the biomass is contained in the above-ground portion of the woody plants. Biomass above ground increases from the northern boreal forest southwards towards the tropics, starting from very low levels at the Arctic tree line, and reaching in excess of 940 t ha^{-1} [838,480 pounds per acre] in the Amazon basin. However, there are exceptionally large forests outside the tropics, notably the temperate forests of the Pacific Northwest of North America. These include stands of huge *Psuedotsuga menziesii* (Douglas fir), reaching 1,600 t ha^{-1} [1,427,200 pounds per acre], and *Sequoia sempervirens* (coastal redwoods), the tallest trees in the world, which have a biomass of up to 3,450 t ha^{-1} [3,077,400 pounds per acre] just in the trunks. Below-ground biomass in roots is significantly less (Jackson et al. 1996), averaging 29 t ha^{-1} [25,868 pounds per acre] in boreal forests, 40 to 42 t ha^{-1} [35,680 to 37,464 pounds per acre] in temperate and tropical deciduous forests, and 49 t ha^{-1} [43,708 pounds per acre] in tropical evergreen forests.

Biomass is a static measure of how much mass there is at any one time, with no indication of how quickly new growth is being added or lost, and so gives little insight into how the forest is functioning. More useful are estimates of the productivity of the forest, i.e. how much new material is being added per year, described as net primary productivity (NPP). This can vary from as little as 1 t ha^{-1} y^{-1} [892 pounds per acre per year] in cold boreal forests, to over 30 t ha^{-1} y^{-1} [26,760 pounds per acre per year] in tropical rainforests, with an average of 7 to12 t ha^{-1} y^{-1} [6,244 to 10,704 pounds per acre per year] in temperate forests. However, a maximum of 36.2 t ha^{-1} y^{-1} [32,290 pounds per acre per year] has been recorded in the Pacific Northwest from a 26-year-old forest of *Tsuga heterophylla* (western hemlock). These figures have sometimes been used to calculate how much additional forest needs to be planted to soak up (sequester) the huge amount of extra carbon that is being pumped into the atmosphere—usually approximately 25% extra forest globally. However, such an estimate is blatantly wrong. When a forest is mature it reaches an approximately steady state of mass, where NPP is balanced by an equal loss in biomass through decomposition. At this point, the productivity of the whole forest (the net ecosystem productivity - NEP) drops to near zero. Thus, it is only young forests that are carbon

sinks; once forests are mature they become carbon neutral. In reality, temperate and northern forests globally are a net sink of carbon, but this is primarily due to expansion of the amount of forest due to reforestation (Beedlow et al. 2004).

LIGHT

Trees have evolved as a life form to outcompete their neighbors for light by growing tall, so producing dense forests that inside are darker, more humid, and less prone to extremes of temperature variation than outside. In temperate forests at least, it is usually possible to recognize four reasonably distinct layers. At the top is the tree canopy, normally 5+ m [16.4 feet or greater] above ground. Below are the shrub layer (<5 m) [less than 16.4 feet], the field or herb layer of herbaceous plants and short woody plants such as brambles, and the ground or moss layer of mosses and liverworts, lichens, and algae. Each layer blocks sunlight so that a dense layer may preclude any layers below, and the forest floor may be very dark indeed. In temperate regions, the amount of light reaching the forest floor may be as high as 20 to 50% of full sunlight in an open birch wood, down to just 2 to 5% beneath *Fagus sylvatica* (European beech). In these deciduous forests, light levels are higher once the leaves have fallen, but the trunks and branches still block some light such that light levels are likely to be below 70 to 80% of full sun. Evergreen forests tend to cast similar shade all year round; in Europe, light levels below natural *Pinus sylvestris* (Scots pine) forests are usually around 11 to 13%, while below *Picea abies* (Norway spruce) they can be as low as 2 to 3%. In tropical rain forests, light levels at the forest floor may be even lower, just 0.2 to 2% of full sunlight.

***Primula vulgaris* (primrose), a wintergreen plant that keeps some leaves alive throughout the year.**

As a rule of thumb, plants require 20% of full sunlight for maximum photosynthesis and at least 2 to 3% sunlight for photosynthesis to exceed background respiratory costs (the compensation point). This inevitably means that the floor of densest forests is at, or beneath, the limits of plant growth. Some forest floor plant specialists have overcome this problem with a number of physiological solutions.

- Using shade leaves that are thinner and more efficient at low light levels than sun leaves.
- Reducing the compensation point. Bates and Roeser (1928) found that coastal redwood in deep shade requires just 0.62% sunlight.
- Making use of sunflecks—patches of sunlight passing through gaps in the canopy—which can briefly give up to 50% of full sunlight and make up 70 to 80% of the total solar energy reaching the ground in a dense forest (Evans 1956). These flecks are especially important to shade plants that are capable of responding quickly to the brief flurries of light.

Plants can also cope with dark conditions by avoidance. Temperate deciduous forests are well-known for their colorful carpets of prevernal plants, which grow and flower early in spring. In the UK these include *Hyacinthoides non-scripta* (bluebell), *Ranunculus ficaria* (lesser celandine), and *Anemone nemorosa* (wood anemone). These plants make use of the light reaching the ground before the trees develop their canopy of leaves, and die back once the shade is too deep. Summergreen plants, such as *Mercurialis perennis* (dog's mercury) and *Galium odoratum* (woodruff), are similar but keep their leaves through the summer using what little light is available. As an extension of this strategy, wintergreen plants (which keep at least a few green leaves all year round) and true evergreen plants can start growth as soon as spring conditions allow, and continue growth into a warm late autumn after leaf fall. Such plants include wintergreen *Oxalis acetosella* (wood sorrel) and *Primula vulgaris* (primrose), and evergreens such as *Hedera helix* (ivy) and *Ilex aquifolium* (holly). Being evergreen is an efficient strategy for coping with seasonally abundant light, but it does carry costs. In winter, holly is a sitting target for herbivores such as deer, and so has evolved prickly spines to the leaves. These spines are absent above deer-browsing height, around 3 m [9.8 feet] above ground.

Tree seedlings face similar problems of shade, having to grow up through dark layers of vegetation before reaching the canopy. Different tree species vary tremendously in how much shade they can bear as seedlings and saplings. *Fagus sylvatica* (European beech) and *Acer saccharum* (sugar maple, from North America) are very tolerant of deep shade, while *Betula* spp. (birches) and *Populus* spp. (poplars) grow best under high light intensities. However, it is now apparent that the ability to tolerate shade can change through the lifespan of a tree (Poorter et al. 2005), so it is possible that many trees are more shade tolerant as seedlings than as adults.

Seedlings of *Fagus sylvatica* (European beech) are very shade-tolerant and capable of growing under the dense canopy of their parents. Each seedling shows two distinctively shaped cotyledons below the young shoot.

Nevertheless, comparatively few trees can tolerate the full shade cast by their mature relatives. Consequently, they depend upon gaps appearing in the forest, by one or more trees dying or falling, for successful establishment of seedlings. Gaps are sufficiently important that while large-scale regional vegetation (e.g., oak forest) is determined by climate, soil, and topography, it is the dynamics of gaps that largely controls the proportions in which the various species grow in any one area. For example, in small gaps created by one tree falling, shade tolerant trees such as *Fagus* spp. (beech) or *Abies* spp. (fir) are more likely to do best and dominate. In larger gaps, species such as *Betula* (birch) and *Salix* (willow),

which invade quickly from light, wind-borne seeds and grow rapidly, are more likely to dominate initially but later give way to shade-tolerant trees. It is not just what goes on above ground that is important; in larger gaps there will also be less below-ground competition from the root systems of the large trees at the gap edge. The importance of such competition has been demonstrated experimentally by cutting roots (trenching) around the edges of a plot: seedlings inside the plot usually grow faster (e.g., Barberis and Tanner 2005). Competition may also happen below ground from the field layer vegetation by allelopathy, i.e., secretion of chemicals, which inhibit other root growth, into the soil (e.g., Orr et al. 2005). Further variability in seedling establishment is produced by small-scale heterogeneity of the forest floor. Pits and mounds of bare mineral soil created by falling trees offer less competition and a more constant water supply than the surrounding humus-rich forest floor. In a *Pinus sylvestris* (Scots pine) forest in Finland, Kuuluvainen and Juntunen (1998) found that although these bare sites covered just 8.4% of the forest, they held 60% of pine and 91% of birch seedlings and saplings. Dense field and ground layers can cause problems for tree regeneration, swamping small seedlings. This is one reason why, in temperate rainforests, seedlings are often most common on "nurse logs," which are continuously damp enough to provide moisture and lift the seedlings above the dense field layer.

As tree seedlings grow upwards into a gap, there can be intense competition to reach and keep the light; whichever seedlings grow quickest will dominate the gap, at least in the short term. A common strategy to get a head start, found in trees as diverse as *Fraxinus excelsior* (European ash), and shade-tolerant firs (Narukawa and Yamamoto 2001), is to have a seedling bank. Here, young plants survive in light conditions below their compensation point (i.e. they are sustaining a net loss of energy) and grow very slowly while their energy reserves last. These seedlings are then able to take rapid advantage of an opening in the canopy in the race for dominance.

WATER

Given that a single, large deciduous tree can use 400,000 liters [105,670 gallons] of water in transpiration in a summer (Thomas 2000), it is obvious that whole forests move immense amounts of water from the soil to the atmosphere. Nevertheless, water is rarely limiting for tree growth in temperate regions until rainfall decreases to such an extent that scrub and grasslands take over. Almost all roots tend to be quite shallow, so potential problems exist if the surface layers of the soil are drained of available water between rain events. This is obviated, however, by the process of hydraulic lifting present in a number of trees and a few grasses. Here, water is raised at night from moist areas lower in the soil (flowing along a hydraulic gradient through the roots) to nearer the surface. Hydraulic lifting is most common in savannas and other xeric (dry) woodlands, especially among older trees (Domec et al. 2004), but is found elsewhere. The amounts moved can be significant: a mature *Acer saccharum* (sugar maple) 19 m [62.3 feet] high can raise around 100 liters [26.4 gallons] of water each night compared to a water loss via transpiration of 400 to 475 liters [106 to 125 gallons] the following day (Emerman and Dawson 1996). This raised water also benefits other surrounding plants (Penuelas and Filella 2003; Filella and Penuelas 2003–2004).

Forests also play a significant role in the redistribution of water on a regional scale. Rainfall intercepted by the canopy is evaporated before it reaches the ground. When this and the transpiration of water are combined (evapotranspiration), the overall losses are in the order of 30 to 60% of precipitation in deciduous forests, 50 to 60% in tropical evergreen forests, and 60 to 70% in coniferous forests, compared to around 20% in grasslands. Not surprisingly, forested areas have water yields (measured as stream flow) 25 to 80% lower than pastures. Moreover, computer modeling by Calder et al. (2003) suggests that planting oak woodland in central England would eventually reduce recharge of aquifers and runoff to streams by almost one half. So, should forest be removed to improve water yield? Most data show that regardless of forest type, removal of up to 20% of the trees has an insignificant effect on water yield, presumably because of increased soil evaporation replacing evapotranspiration (Brown et al. 2005). Further clearance does improve water yield (Bosch and Hewlett 1982), but by comparatively small amounts until clearance is significant.

Many people have held the view that forests increase rainfall in a watershed through evaporating water, thus helping build clouds. However, in temperate areas, at least, the contribution of a forest to rainfall is likely to be insignificant and certainly less than 5% (Golding 1970). On a continental scale, forests help to increase rainfall in the sense that they repeatedly recycle the atmospheric moisture passing from the oceans to the land. For example, in the Amazon Basin, much of the daily rainfall is immediately evaporated to generate clouds for rainfall downwind. It is highly likely that continual clearance of the forest will reduce rainfall elsewhere in the region since much of the water will enter rivers and be lost to the system. Moreover, the effects of such tropical deforestation have far wider repercussions in mid- and high latitudes through large-scale links in the water cycle and weather. Avissar and Werth (2005) have shown, for example, that deforestation of Amazonia and Central Africa severely reduces rainfall in the Midwest of the United States.

NUTRIENTS

Nitrogen is usually the nutrient most limiting growth in temperate forests, while in other forests, especially on soils of great age, phosphorus may well be the limiting nutrient. Nutrients within a forest ecosystem are highly recycled and key to this recycling are the decomposer organisms that release nutrients from dead material. Larger soil fauna, such as earthworms and beetles, chew debris into fine particles suitable for the soil fungi and bacteria. A square meter of soil in temperate woodland may contain more than 1,000 species of animal, from protozoa to earthworms, and a gram of soil can contain more than 1,000 species and more than 200 million bacterial cells (Fitter, 2005).

Soil organic matter (surface litter and humus incorporated into the soil) is thus the main bottleneck controlling nutrient availability to plants, and the slower decomposition is, the more of a limiting factor it is. This helps explain why slow plant growth occurs on cold northern soils that have large organic matter accumulations.

Fungi and bacteria are not altruistic in providing nutrients to plants. As dead material is decomposed, nutrients released by the microorganisms are immediately taken back up by other microorganisms, and so are effectively immobilized and unavailable to plants. However, as the carbon is progressively used up in their

respiration (and released as carbon dioxide), the conserved nutrients become more than the microbes can use, and the excess is released in inorganic form for plants to use. Consequently, when a fresh batch of litter arrives on the forest floor there is a variable time lag before its carbon has been reduced sufficiently to allow nutrients to be freed into the soil for plant growth, the process being regulated by the microbial community (Attiwill and Adams 1993; Agren et al. 2001). Plants can, however, circumvent this bottleneck in several ways. Firstly, more than 80% of the world's vascular plants have on their roots mycorrhizal fungi, which greatly assist in scavenging nutrients from the soil to the symbiotic benefit of both plants and fungi. Secondly, some plants are now known to be able to directly use organic nutrients, without the intervention of microorganisms first breaking them down into inorganic forms. For example, up to 50% of the total nitrogen in forest soils is usually in the form of dissolved organic nitrogen (DON), of which approximately 10 to 20% consists of amino acids. The degree to which plants can use DON is open to speculation, but it is becoming clear that many plants are capable of absorbing amino acids directly (Lipson and Nasholm 2001) and are thus able to short-circuit the microorganism bottleneck. The same may also be true for organic phosphorus.

Although nutrients are tightly recycled within a forest ecosystem, there are still (usually small) annual inputs and losses. Nutrients are added to forests

The effect of 14 years of nitrogen enrichment on *Pinus resinosa* (red pine) at Harvard Forest: (top) control plot with no extra nitrogen added above the background deposition of 7 to 8 kg N ha^{-1} y^{-1}; (middle) low N addition (50 kg N ha^{-1} y^{-1}); and (bottom) high N addition (150 kg N ha^{-1} y^{-1}).

through rain and dust, dissolved from rocks in the soil, and as biological input from nitrogen fixation by microbes. Losses of nutrients can be very rapid due to fire, wind, and erosion but the majority of losses, from temperate forests at least, are by leaching of nutrients as water percolates through the soil. However, since nutrients are vital to forest growth, plants and microbes are fairly efficient at reabsorbing and holding available nutrients and creating conditions of controlled decomposition. This has been admirably demonstrated by the Hubbard Brook Ecosystem Study in the White Mountain National Forest of New Hampshire, established in 1963 (Likens 2004). As part of this, a discrete watershed was clear-felled in 1965–1966 and treated with herbicides for three years to prevent any regrowth, while a similar watershed had the hardwood forest left intact. After clear-felling, stream flow went up (due to reduced evapotranspiration) and net losses of nitrate, calcium, and potassium in stream water generally peaked in the second year, each returning to pre-cutting levels at rates unique to each ion as the forest regrew. However, even decades after clear-felling, differences in stream water solutes can still be seen, especially in calcium (Likens et al. 1998).

There is still a good deal to learn about mechanisms of nutrient retention in forests. For example, Muller and Bormann put forward the vernal dam hypothesis in 1976. This proposes that prevernal plants, which grow early in spring before canopy closure, take up nitrogen and other nutrients before they can be leached; these are subsequently made available to other plants as the prevernal plants die back from lack of light. At Hubbard Brook, plants of *Erythronium americanum* (yellow trout lily) saved almost half of the important nutrients from being washed away. In the spring they used 43 and 48% of the released potassium and nitrogen, respectively, with the rest being lost in stream water. Some subsequent experiments (e.g., Tessier and Raynal 2003) have supported the theory. However, other contradictory studies have shown that the microbe population itself is better at soaking up the spring burst of nutrients (e.g., Zak et al. 1990). Also, while the dying back of vernal plants can produce a burst of nutrients (e.g., Anderson and Eickmeier 2000), the plants may not be very efficient at taking up nutrients in the first place (e.g., Anderson and Eickmeier 1998; Rothstein 2000). Undoubtedly, some of the experimental differences come from investigating different plant species in several forests. The tight recycling of nutrients within the forest ecosystem can cause problems if too much arrives as pollution. Nitrogen enrichment, particularly in northern temperate areas, is just such a case (Nosengo 2003). Since the 1980s, normal background nitrogen deposition of <1 kg ha^{-1} y^{-1} [less than .892 pounds per acre per year] has increased by 10 to 40 times or even higher. The effect of too much nitrogen is clearly seen in long-term experiments running at Harvard Forest, Massachusetts since 1988 (Magill et al. 2004). In one of these, a plantation of *Pinus resinosa* (red pine) was subjected to three levels of nitrogen: a control, low N addition, and high N addition. After 14 years, annual wood production had decreased by 31% and 54% relative to the control in the low N and high N plots, respectively, and the canopies had thinned due to dieback under higher nitrogen levels. Mortality also increased (control 12%; low N 23%; high N 56%) and the whole high N stand was expected to die in the near future.

COARSE WOODY DEBRIS

The vital importance of dead wood in forest carbon budgets, and also as an invaluable wildlife resource, has been increasingly appreciated over the last decade (Kirby and Drake 1993). Dead wood appears in many forms, sizes, and positions including standing dead trees (snags), dead branches in the canopy, and trunks and branches on the ground. A useful term for this motley collection is coarse woody debris (CWD). Typically, CWD in a forest forms up to a quarter of all the above-ground biomass and is normally in the range of 11 to 38 t ha^{-1} [9,812 to 33,896 pounds per acre] in deciduous forests, with the largest amounts in cooler regions where decomposition is slower. Conifer forests generally hold more CWD than deciduous forests, typically around 100 t ha^{-1}, [89,200 pounds per acre] but up to 500 t ha^{-1} [446,000 pounds per acre] in the coastal redwood forests of California and the rain forests of the Pacific Northwest. Tropical forests, with more rapid decomposition, usually have lower amounts of woody accumulation, but levels up to 100 t ha^{-1} [89,200 pounds per acre] are possible in more water-logged areas of the Amazonian forest. If 100 t ha^{-1} [89,200 pounds per acre] of wood was spread evenly over the forest floor it would amount to 10 kg [22 pounds] in each square meter. However, because the bulk of the wood is in large pieces, typically less than 5% of the ground will be covered by CWD, although this can rise to around a third cover in very dense coniferous forests. Snags are of particular wildlife interest. In the Bialowieża forest of Poland, one of the most pristine forests in Europe, Bobiec (2002) found that standing dead wood varied from 3 to 21% of total CWD, and figures of 25% are typical in many of the world's forests.

Wood is difficult to decompose. It is composed of 40 to 55% cellulose, 25 to 40% hemicelluloses, and 18 to 35% lignin (conifers having a greater proportion of lignin than hardwoods). Wood is thus high in structural carbohydrates (which require specialized enzymes to break them up) but also poor in nutrients such as nitrogen: 0.03 to 0.1% N (by mass) compared to 1 to 5% in foliage.

In most forests, wood (CWD) will be colonized by fungi within a year and completely colonized within 5 to 10 years. However, decay rates of wood vary tremendously depending upon the climate, decaying organisms available, and the size and type of wood. In general terms, pioneer trees such as birches and willows invest less energy in protecting their wood from rot (going for

Temperate rain forests, such as the one here on western Vancouver Island, Canada, can contain large quantities of dead wood, in part because of the size of some of the fallen logs. The one shown here is of *Picea sitchensis* (Sitka spruce).

speed of growth rather than defense) and logs on the ground rot away within a few decades. Wood from longer-lived trees such as oaks may persist for a century or much longer, while in cool climates such as the Pacific Northwest wood may persist for up to 600 years (Franklin et al. 1981). Even in tropical rain forests, wood above 3 cm [1.2 inches] diameter takes at least 15 years to decompose (Anderson and Swift 1983). Again, however, environmental conditions play an important role in determining decay rates; logs of *Populus balsamifera* (balsam poplar) in North America, which would decay away within 40 to 60 years on land, last for over 250 years when waterlogged in a beaver pond.

EVERGREEN AND DECIDUOUS LEAVES

At first sight, the occurrence of evergreen and deciduous trees in different forests can appear haphazard, but in reality it demonstrates the interactions of many of the ecological processes described above (Thomas 2000). Deciduous trees lose their leaves during an unfavorable season (winter in temperate areas), while evergreen trees always have some leaves on the tree and individual leaves may live from six months to over 30 years. If growing conditions are favorable all year round, as in tropical rain forests, then there is no selective advantage in being deciduous and so evergreen angiosperms dominate. In climates with a dry summer or cold winter, it is cheaper to grow thin disposable leaves than to grow more robust leaves capable of surviving the off-season, so in most moist temperate areas deciduous trees dominate. However, if environmental conditions become worse, it may once again be more beneficial to grow evergreen leaves. This includes areas with a very short growing season, where evergreen leaves are able to start growing as soon as conditions allow and so none of the growing season is wasted.

Evergreen conifers, such as *Abies lasiocarpa* (subalpine fir) shown here in the Canadian Rocky Mountains, are typical of areas with short growing seasons where deciduous trees are disadvantaged by wasting part of the season producing new leaves.

Deciduous forest in Harvard Forest, Massachusetts, USA. In a seasonal temperate climate it is more economical for trees to grow a set of disposable leaves each spring rather than build leaves capable of surviving the winter.

In the very short growing season of the tundra overlying permafrost, evergreen shrubs give way to deciduous *Salix* spp. (willows). (The graves are those of 19th century whalers who overwintered and died here on Herschel Island in the Arctic Ocean.)

This accounts for evergreen leaves in northern and alpine areas, and also among woodland understory shrubs such as holly and ivy, which benefit from an early spring start and late autumn finish when the canopy has no leaves. Evergreen leaves are also found in Mediterranean climates where the winter growing season is dry; leaves that are protected enough to cope with the droughty conditions will also survive the hot dry summer, and so effectively become evergreen and need to be kept for several years to repay the high investment cost. In areas where the climate becomes even more severe, such as at the Arctic tree line or in alpine areas, deciduous leaves re-appear. Despite the problems of a very short growing season and acute shortage of nutrients, the winter is so severe that it is cheaper to build new leaves every year rather than attempting to keep leaves alive. Thus, the northernmost trees in the Arctic and uppermost trees in alpine areas are deciduous trees such as species of *Betula* (birch), *Larix* (larch), and *Salix* (willow).

CONCLUDING REMARKS

Forest ecosystems work in much the same way as any other ecosystem, but size and complexity create ecological situations that are unique to forests. The large amounts of biomass that can be grown in a year appear useful for carbon sequestration in relation to global warming, but must be weighed against the decompositional losses in mature forests, and possibly the extra methane—a potent greenhouse gas—that these will generate (Keppler et al. 2006). To maintain sequestration rates, new forests are constantly needed. Light availability presents problems for those plants living below the dense forest canopy, but these problems are solved by making do with less light or growing when light is available in the spring or during brief sunflecks. The role of forests in the water cycle still needs to be fully clarified, but it is of great importance due to the likely pressure on forests as human water needs increase. Nutrient dynamics in forests are crucial to their long-term well-being and it is important that we improve our understanding of the effects of climate change and pollution on decomposition and nutrient cycling. Of necessity, this chapter gives only a resume of a very large subject. A more detailed account of forest ecology is provided by Thomas and Packham (2007).

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A Taste of Sichuan: *Zanthoxylum simulans*

Jonathan Damery

Spices have molded the modern world. Columbus and his fleet sailed in the name of black pepper. New Amsterdam, the Dutch colonial settlement on Manhattan Island, became New York in an island trade essentially pertaining to nutmeg. And the records go on back, to the time when the caravan routes of the rising Arab world first introduced exotic Eastern spices to the insipid foods of Europe.

The worldwide distribution of spice-producing plant species (and especially the woody plants within that group) is limited mostly to tropical climates, which excludes the most common spice plants from the temperate-zone tree and shrub collections of the Arnold Arboretum. Of the few exceptions, the Arboretum is home to one spice-producing plant of particular interest—*Zanthoxylum simulans,* a source of Sichuan pepper.

Though not a common spice in American kitchens, the signature mouth-numbing flavor of Sichuan pepper is indispensible in the regional cuisine of Sichuan, China. It is produced from the dried fruit of several different species of *Zanthoxylum,* also known as the prickly ashes. The most common sources are *Z. bungeanum* and *Z. simulans* (formerly considered varieties of the same species), and *Z. piperitum* is used for similar culinary purposes in Japan.

IT IS INTERESTING to note that *Zanthoxylum* is a member of the citrus family (Rutaceae). In the United States, this relationship has proved to be rather problematic for Sichuan cooks. Thought to be a potential mode of introducing citrus canker to American citrus groves, the United States Food and Drug Administration forbade its importation for nearly forty years, from 1968 to 2005 (though serious enforcement only came about in 2002). The ban was lifted under the stipulation that the Sichuan pepper be heated just enough to kill any infectious bacteria prior to importation.

Several examples of both *Zanthoxylum simulans* (flatspine prickly ash) and *Z. piperitum* can be found growing in the Arboretum, but the most notable is a large specimen of the former, tucked in just before the smoketree collection on Meadow Road. This specimen (accession 1803-77-A) was collected as seed by Arboretum taxonomists Stephen Spongberg and Richard Weaver in 1977 from the Forest Research Institute in Seoul, South Korea.

The gracefully spreading form of this specimen (24.3 feet [7.4 meters] tall, 6.5 inch [16.5cm] diameter main stem) melds easily into the border of Meadow Road, but even in the winter it is worth taking a few steps off the path for a closer view. A spiny plant from twig to trunk, the spines (or technically prickles in the case of those on the trunk) become enlarged and woody, lending an exotic appearance to the tree. The deep green compound leaves have an attractive glossy sheen, and in midsummer *Z. simulans* is covered with a greenish white haze of small flowers, followed by a prolific display of small, round follicles (a type of dehiscent fruit). At maturity these fruits turn a pinkish-bronze color and split open, spitting out the seeds. The dried follicle is the culinary product, Sichuan pepper.

On the plains and in upland forests of northern and central China, Arboretum plant explorer E. H. Wilson reported that *Zanthoxylum simulans* grew naturally on cliffs and waysides. In cultivation it was grown in dry, hot river valleys. This is a good indication of its adaptability to a myriad of difficult landscape conditions. The species is cold hardy in USDA Zones 5 to 7 (average annual minimum temperature -20 to 10°F [-28.8 to -12.3°C]).

From the bare winter trunks through the remarkable autumn fruit display, *Zanthoxylum simulans* is worth viewing all year long. It is a not-so-hidden—but often missed—Arboretum treasure.

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