

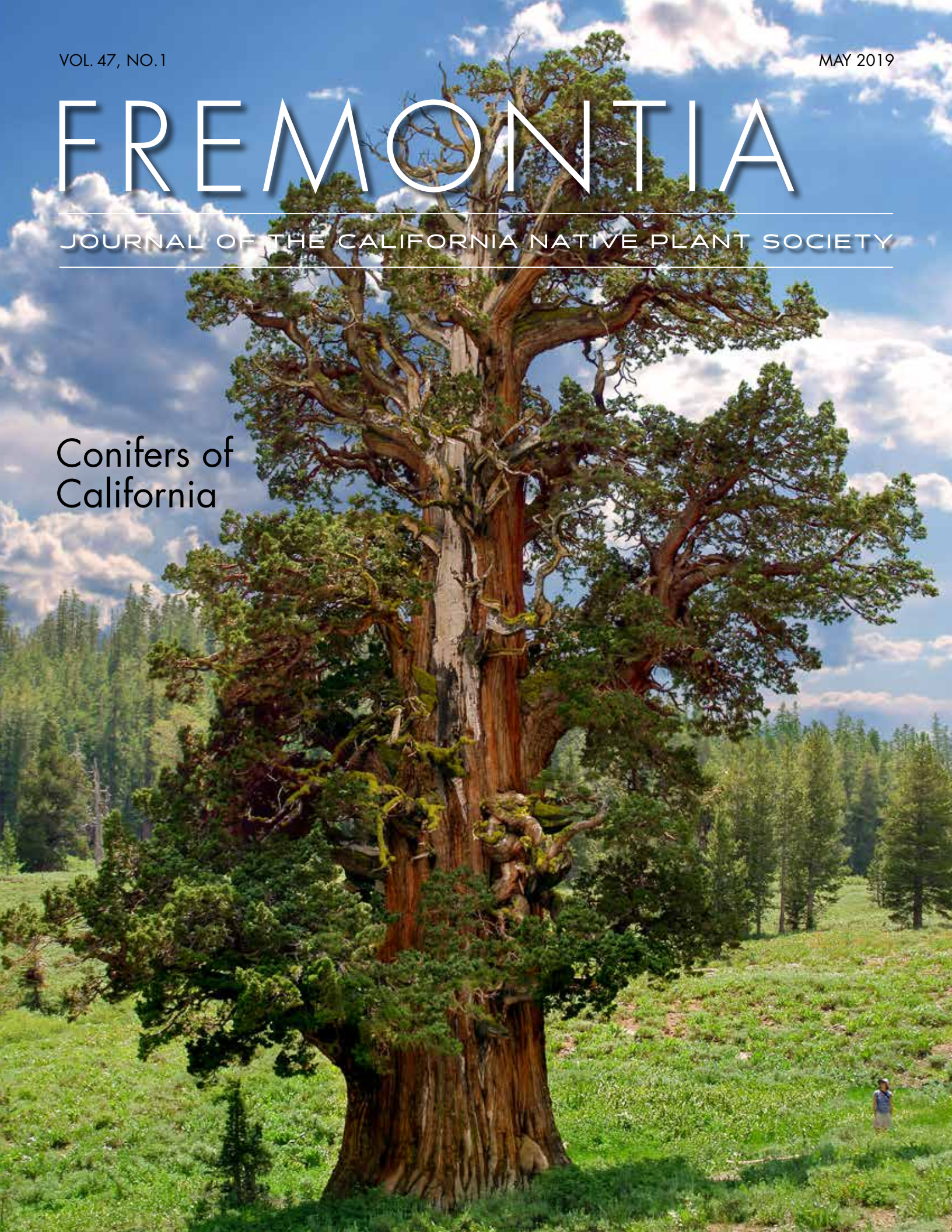
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FREMONTIA

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Conifers of
California





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FREMONTIA

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FROM THE EDITOR

“Conifer” means “cone-bearing” in Latin (*cones*=cone; *ferre*=to bear). So conifers are, with a few exceptions (think yew), plants that bear cones. At one time, long long ago, before any of us were born, conifers and other gymnosperms (naked seed-bearing plants) ruled the earth. That was in the Mesozoic era (250 to 65 million years ago). The flowering plants didn’t really become dominant until the Cenozoic.

But there are still large parts of the planet—particularly in the northern hemisphere—where conifers rule. And we who live in California don’t even need to travel to the taiga to encounter such places. Just think of the great pine, fir, and cedar forests of the west slope of the Sierra Nevada. And the majestic coast redwood and Douglas-fir forests of the north coast. We probably don’t think of the scrubbier, sparser woodlands of the High Sierra or southern mountains or central coast, and of the conifers that inhabit them. But we should. The authors of this conifer-focused issue of *Fremontia* certainly have, devoting great parts of their lives to studying, and helping the rest of us understand, these less charismatic members of the conifer family.

I’ve learned a lot working on this issue as guest editor over the past six months. Particularly from those authors, all of them dedicated scientists who were incredibly patient working with this non-scientifically-trained visitor from the world of nature publishing (I was the cofounder and publisher of *Bay Nature* magazine for 17 years). All of them have contributed their knowledge, time, and expertise to *Fremontia* for free, in order to share the information they have spent months and years collecting and analyzing. Their work helps us better understand both the immensely rich and diverse natural treasures in this state, and the magnitude of the task we all face—scientists and non-scientists alike—in protecting them in a rapidly changing climate.

So a big thanks to the authors. And to the photographers, who also contributed their work for free. And to all of you readers and CNPS members for supporting this brand of serious, science-based journalism about the part of the world we inhabit.

- David Loeb, *Guest Editor*

Cover: Sierra juniper (*Juniperus occidentalis* var. *australis*) is the world’s largest juniper species. And the Bennett Juniper, growing in a private inholding within the Stanislaus National Forest in Tuolumne County, is by far the largest of its species, with a diameter of 389 centimeters. [Robert Van Pelt]



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Monterey cypress trees at Point Lobos [Arlyn Christopherson]

INTRODUCTION: CALIFORNIA CONIFERS

by Ronald M. Lanner

If this issue of *Fremontia* had appeared when I first arrived in California in 1958 it would have featured a different cast of coniferous characters. California was then a prolific timber producer. A three-log load of Douglas-fir was all it took to fill the bunks of a logging truck barreling down the west slope of the Sierra Nevada. Big “sticks” of ponderosa and sugar pine made their way to countless sawmills to be milled into construction lumber; massive incense cedars were reduced to many millions of pencils, posts, and grape stakes. On

the north coast, fog dripped much of the year from foliage of arrow-straight coast redwoods that reached for the sky while awaiting felling by hard-hatted workers; and in scattered Sierran groves giant sequoias presented impossibly massive trunks to tourists who made pilgrimages to them and built California’s renown for majestic forests around the world. I arrived, serendipitously, as newly-discovered bristlecone pines exceeding 4,000 years of age on summits of the White Mountains were being heralded on the pages of *National Geographic* as “the world’s oldest living things.” California’s conifer forests kept getting more interesting.

Since then, our knowledge of this state’s native conifers has broadened, as reflected in this issue of *Fremontia*. Today we regard all the trees of our forested ecosystems as valuable and essential members. We still honor great size and age, as attested by Robert Van Pelt’s descriptions of our state’s largest trees. But most of our authors are preoccupied with questions of morbidity and survival in some decidedly non-charismatic species (limber pine, anyone?) serving as the canaries in our coal mines in a time of global climate change.

In their article, “Forest Resilience and Mortality in the Sierra Nevada,” Jodi Axelson and her co-authors focus on the factors affecting morbidity in a forest. Under relatively benign disturbance regimes, mortality occurs at low background rates, but these can be exceeded by more massive pulses of mortality and dieback, and that is a major concern in our climate change era. An interesting innovation in analyzing tree mortality by these authors is the concept of a “death funnel” in which a tree’s risk of death increases as it descends down the funnel, becoming more susceptible to potential mortality agents.

The gloomy prospect of the Sierra’s impressive forests descending the death funnel is somewhat leavened by the stories of gigantic trees that have been documented from the past, and many that survive or are even being newly discovered. Robert Van Pelt’s article, “Revisiting California’s Big Trees: A Selective History,” triggers at least a modicum of optimism while at the same time documenting the tragic extractive history that has removed many of these giants from our midst.

Van Pelt’s article reminds us that California is home to the largest, tallest, and oldest trees that inhabit this planet, including the largest individuals of five conifer genera: a pine and four members of the cypress family. It was, in fact, some of these giant trees that inspired the birth of an ethos of conservation in the state, a heritage highlighted by last year’s centennial celebration of the founding of Save The Redwoods League. In her interview with editor David Loeb, that venerable organization’s science director, Emily Burns, discusses the group’s Centennial Vision, giving us reason to hope that our optimism will not itself go down a death funnel.

But, again, it is the stories of some of the less well-known California conifers that this issue of *Fremontia* seeks to bring to the fore. Such as the whitebark pine. A fruitful collaboration of plant and animal biologists has identified and clarified the coevolved mutualism of whitebark pine and Clark’s nutcracker. Briefly stated, the pine provides high-energy nutrition (seeds rich in fats and protein) to the nutcracker, and the nutcracker shallowly caches in the soil those seeds it does not immediately eat, making them available for later seedling recruitment. The relationship is mutualistic, and no other means of dispersal and establishment have been identified for whitebark pine.

Ironically, as these facts were being illuminated in the 1970s, darkness was starting to descend, in the form of white pine blister rust, mountain pine beetle, and wildfire. Thus the mutualistic partners were soon put in peril. This is especially the case in the Rocky Mountains, where the pine and its disperser are more widespread, but mortality has been increasing recently in the Sierra Nevada and Cascades. The article, “Subalpine Sentinels,” by Michèle Slaton reviews the current health and status of this species in our state and concludes that continued monitoring is both justified and necessary to plan future management actions.

Another example of pine-nutcracker mutualism is that of Clark’s nutcracker and limber pine. Limber pine has evolved fewer morphological adaptations to seed harvest by the nutcracker than has whitebark pine, but it does appear dependent on the nutcracker for seed dispersal and seedling establishment. Therefore both whitebark and limber pines can only grow where the nutcracker caches their seeds, a key point in the distribution of both pines. So it’s no surprise that Constance Millar has found limber pine not responding in a stereotypical way to climate change. In her article “Limber Pine’s Wild Ride With Climate,” she shows that this pine does not simply “shift up in elevation as temperatures warm.” Rather, using dendrochronological and demographic techniques, Millar finds its occurrence correlated with actual microclimatic conditions at the growing site, not theoretical lapse rates or generalized regional conditions. This suggests the need for continuing study in the field to identify potential refugia that could be significant for future limber pine populations.

For the past decade Piute cypress and its North American relatives have struggled to exchange the hallowed generic name *Cupressus* for the less mellifluous *Hesperocyparis* in order to accommodate new findings suggesting a single origin for the New World cypresses. The distinction, made mainly on molecular evidence, has the potential of clarifying an historically confusing systematic situation among California’s second richest genus of conifers. As pointed out by Jim Bartel in “Piute Cypress: An Interesting Past and Troubling Future,” this small unprepossessing cone-bearer is endemic to Kern and Tulare Counties where it is found in small groves at middle elevations on a variety of mainly granitic soils. Like California’s other cypresses, Piute cypress has serotinous cones, meaning they remain on the tree, closed, with the intact seeds inside, until their release is triggered by the melting of resin that bonds the cone scales. Thus the species is adapted to regenerating after fires. However, wildfires have been increasing in frequency and severity, often destroying trees before they become reproductive. Bartel’s article is followed by a photo gallery of the nine other California species of *Hesperocyparis*, perhaps the first to display them all together under their new generic epithet.

The phenomenon of serotiny also distinguishes California’s closed-cone pines, an informal category that includes Monterey, bishop, and knobcone pines. Matthew Reilly profiles the latter in his article, “Ready to Burn.” As he details, the natural history of this species, and of other serotinous conifers, is more complex than usually depicted. For example, Reilly suggests that “partial serotiny” is an adaptive strategy to take advantage of variable and unpredictable fire-return intervals, and he distinguishes necriscence (cone-opening following tree death) and xeriscence (cone-opening following drought) from routine opening. Nailing down the mechanics and ecological significance of these natural history traits should keep researchers of serotiny busy during long fire intervals. And may even serve to recruit new researchers to the fascinating realm of California’s astonishingly diverse conifers, for which this issue of *Fremontia* should serve as a fine introduction.

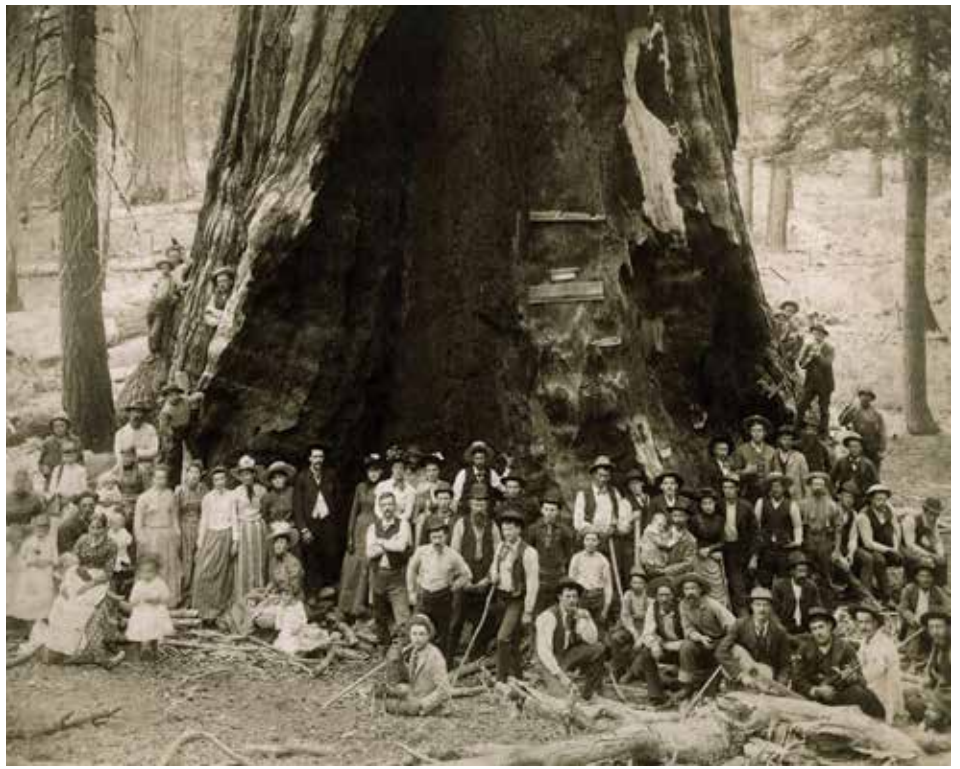


Monterey cypress seed cones [Glenn Keator]

“California is home to the largest, tallest, and oldest trees that inhabit this planet, including the largest individuals of five conifer genera.”

Special thanks to our friends at **Save the Redwoods League** whose generous sponsorship and contributions helped make this issue possible. Since 1918, Save the Redwoods League has protected more than 200,000 acres of redwood forest and helped create 66 redwood parks and preserves in California. Learn more at savetheredwoods.org.





REVISITING CALIFORNIA'S BIG TREES: A SELECTIVE HISTORY

Robert Van Pelt

California, with its great biological diversity and ideal growing conditions, has the largest, tallest, and oldest trees on the planet, all of them conifers. These include the largest individuals of five conifer genera—*Calocedrus*, *Juniperus*, *Sequoia*, and *Sequoiadendron* in the Cupressaceae, and *Pinus* from Pinaceae. In fact, the three largest pines in the world (sugar—*P. lambertiana*; ponderosa—*P. ponderosa*; and Jeffrey—*P. jeffreyi*) are all found in California, as are the tallest individuals of these species. And while the world's largest firs (noble firs—*Abies procera*) are found in Washington, the second and third largest members of the genus are found in California, in Yosemite National Park: California red fir (*A. magnifica*) and California white fir (*A. lowiana*). In the following article, I will share some of the interesting stories behind several of our state's record large trees.

NATIONAL REGISTER OF BIG TREES

American Forests is a conservation organization formed in 1875, known originally as the American Forestry Association. Since the late 1890s the organization has published *American Forests*, a general

audience magazine focused on forest conservation. From time to time the magazine ran short stories on amazing trees encountered across the United States, which were quite popular with the readers. So, in the April 1940 issue, the editors posed a question to the readers: "Where are the largest trees in the country?" A year later, in the April 1941 issue, the first list of the nation's largest trees appeared. This marked the birth of the **National Register of Big Trees**. It was two pages long and featured 77 trees from 24 states. A dozen of these trees—including four in California—were still around when I caught the "bug" and began my big tree adventures in the early 1980s, and I subsequently visited each of them. Today the register includes nearly 800 trees from all corners of the country. In fact, each state now has its own big tree register coordinator, and many states maintain state registers of their own, including California. For many species, especially small or rare ones, the National Register is one of the few sources of reliable information on maximum tree dimensions.

Above left: Figure 1. Bennett Juniper. Sierra junipers are usually found on steep, rocky cliffs, or other places that seem completely inhospitable for tree life, so to see this giant by itself in a rolling meadow makes for a once-in-a-lifetime experience. [Robert Van Pelt]

Above right: Figure 4. An 1890 photo of the General Grant Tree by C.C. Curtis. Even though a large portion of the base of the tree has been burned away, General Grant still has the largest base of any giant sequoia. [C.C. Curtis, California History Section Picture Catalog: California State Library.]

Since the beginning, people have had difficulty defining what constitutes “largest”; i.e., how does one compare a short, fat tree with a tall, skinny tree? In forestry, tree sizes are often determined using wood volume, which can then be converted into biomass. Unfortunately, accurately measuring volume is an extremely difficult process that involves very specific (and expensive) equipment. American Forests solved this problem for the purposes of the National Register by creating a user-friendly point system—requiring the relatively simple measurement of trunk circumference, tree height, and crown spread. One AF Point is given for each inch in trunk circumference measured at breast height (1.37 meters or 4.5 feet above the ground), one point for each foot in height, and one point for every four feet of average crown spread.

Once the first National Register was printed, interested folks had a target, and many initial champions were quickly displaced by larger trees. Now, after nearly 80 years, the register has filled out—finding new champions now is extremely difficult, and if a champion dies, there are usually runners-up already measured ready to claim the throne.

Growing up in the Midwest, I was a math nut obsessed with extremes—largest, tallest, longest, etc. My favorite books were the *Guinness Book of World Records* and the *World Almanac*. My passion for all things arboreal moved to the foreground about 1980, and my awareness of the National Register of Big Trees followed in 1981. Since the Register combined two of my favorite things—trees and numbers—I was hooked. I nominated my first National Champion trees in 1986, and over the past three decades have nominated 92 trees that at one time have been National Champions.

In this article I will focus on four California species with interesting but very different champion tree stories: Sierra juniper, giant sequoia, sugar pine, and ponderosa pine. You will no doubt notice—and wonder why—I have omitted coast redwood (*Sequoia sempervirens*), the world’s tallest tree, from this account. The redwood does indeed have a fascinating story to tell, but because the National Register is about big trees, and not specifically tall trees, I will leave that engaging yet complicated story for another time.

THE TREES

I. Peerless Bennett Juniper

Our first featured champion tree represents one extreme of the National Register—a tree that was on the very first list and has remained the unchallenged champion

Figure 2. Mother of the Forest – 1865. Bark was carefully removed to 37 meters and shipped overseas where it was prominently featured as the Mammoth Tree from California in a section of the great Crystal Palace in London (Inset). [P.H. Delamotte, English Heritage NMR.]



ever since. The Sierra juniper (*Juniperus grandis* or *J. occidentalis* var. *australis*, depending on the source) is the world’s largest juniper species, and the **Bennett Juniper**—located in a private inholding within the Stanislaus National Forest in Tuolumne County—is unrivaled in size [Figure 1]. Sierra junipers can be quite charismatic and, due to their extreme longevity and often exposed locations, they can become quite large and every bit as gnarly as any alpine tree. The Bennett Juniper stands out among its peers: After decades of searching Sierra mountain habitats, no one has found a juniper that even comes close to its dimensions. While this amazing tree is not particularly tall for a “giant”—measuring 24 meters—its trunk has an immense diameter of 389 centimeters.

Since there are Native American bedrock mortars and caches of obsidian nearby, the tree has probably been known to people living in the area for centuries. The first Euro-American record of the tree dates to the 1920s, when sheepherders mentioned it to Clarence Bennett, a naturalist who studied junipers. Impressed, he became an outspoken champion of the tree and fought to get it protected. The Forest Service named the tree after Bennett in the 1950s and it is currently under the protection of Save the Redwoods League.

The world’s oldest recorded juniper is also a Sierra juniper, called the **Scofield Juniper**, coincidentally located only 16 kilometers away from the Bennett. Scofield has a crossdated age of 2,675 years (crossdating is a complex procedure that allows specific calendar years to be assigned to individual tree rings) but its trunk diameter is less than half that of the Bennett. Interestingly, we don’t know—and never will—the full age of the Bennett; dendrochronologists cored the tree



Figure 3. An 1861 portrait of Galen Clark and the Grizzly Giant. Photographer Carleton Watkins deserves significant credit for the initial creation of Yosemite Park in that his were the first photos of giant sequoia seen by the outside world. [C. Watkins, Getty Museum, Los Angeles.]

in the 1930s and again in 1989 in an effort to determine the age, but the tree is hollow, so it's not possible to get a true reading. However, researchers were able to conclude that the tree is at least 2,200 years old.

II. "Big Trees" – The Giant Sequoias

Our second featured champion tree is the giant sequoia (*Sequoiadendron giganteum*)—the world's largest tree species. Giant sequoias are found in the Sierra Nevada range of California in 67 distinct groves that range in size from six trees to 1,600 hectares. This feature of growing in discrete groves is strange considering that all associated tree species have large and contiguous distributions. However, an unusual feature that all giant sequoia groves share is available water throughout the growing season.

The first outside word of the existence of giant sequoias came from the *Sonoma Herald* in June of 1852, when the story of A.T. Dowd's discovery of the giant trees at Calaveras was printed and quickly captivated the world. The small grove he visited occupies only 24 hectares and was originally called the **Mammoth Tree Grove** but is also known as the **Discovery Grove** and is now called **North Calaveras Grove**.

Within a year, loggers expended great effort to cut down the largest tree in the grove. Initially called the **Original Big Tree**, and later the **Discovery Tree**, the chosen tree had a trunk diameter of more than 800 centimeters. Since saws large enough to do the job did not yet exist, the loggers perforated the tree with hydraulic

augers; even so, it took several days of work before the tree finally was brought down. While the **Discovery Tree** had the largest base of any tree in the grove, the largest tree by wood volume (~850 m³) was one called **Mother of the Forest**. In 1854, loggers stripped off the lower 37 meters of its bark to be shipped around Cape Horn and then dramatically reassembled at the Crystal Palace in London for the first World's Fair [Figure 2]. It remained on display until being destroyed by fire in 1866.

The second giant sequoia grove to be "discovered" by Euro-Americans may have been the **Mariposa Grove**, in what is now Yosemite National Park, in 1857. The Mariposa Grove was only 25 kilometers from Yosemite Valley, which was already famous thanks to the dramatic illustrations by Thomas Ayres, who first entered the Valley in 1855.

Photographer Carleton Watkins arrived in Mariposa Grove with his camera in 1861, and his photos of **Grizzly Giant** (which often included the grove's single human inhabitant—Galen Clark) and nearby Yosemite Valley fascinated the nation [Figure 3]. Grizzly Giant had a massive base with a diameter of 820 centimeters, huge fire caves, a dramatic lean, and a gnarled crown; it soon became a Mecca for photographers and tourists. Photos of the Grizzly Giant appeared worldwide, and it became—and still is—one of the two or three most visited trees on the planet.

Abraham Lincoln was so inspired by the images from Ayres and Watkins that, in 1864, he moved to create the world's first nature park by granting the lands of Mariposa Grove and Yosemite Valley to the State of California for permanent protection. This was the first time in history that a national government set aside scenic lands simply to protect them in perpetuity.

Upon completion of the First Transcontinental Railroad in 1869, the giant trees at Calaveras and Mariposa became go-to destinations for travelers from the East. The Grizzly Giant's newfound status as the world's largest tree was to be short-lived, however, as still larger sequoias were soon found in then-undiscovered groves further south in what would become Sequoia and Kings Canyon National Parks.

Perhaps the first of the larger trees in the southern groves to be discovered was one that, to this day, has the largest base of any (911 centimeters in diameter)—the **General Grant Tree** [Figure 4]. The first Euro-American sighting of this tree is credited to Joseph Hardin Thomas in 1862, and the Grant Tree was well known by the time John Muir saw it in 1873. Even then, its condition caused him consternation, as he

wrote that the tree had been “barbarously hacked and engraved with people’s names—chips and bark carried away as mementos.”

Logging interests were soon salivating at the prospect of the timber available in the extensive forests of large conifers in the drainages of the Kings, Kaweah, and Tule Rivers. However, this was some of the steepest terrain in the Sierra Nevada, and the canyons were formidable obstacles. In addition, even though the land had theoretically been for sale by the government since California statehood in 1850, the General Land Office surveys needed before sales could occur did not happen in the southern Sierra until the mid-1880s.

Once land did become available, a mini-land grab ensued. However, conservationists who were concerned about the potential decimation of the majestic trees introduced a bill in Congress to place the General Grant Tree and other nearby giant sequoia groves into a national park. In early October 1890, President Benjamin Harrison signed bills for the creation of three national parks (General Grant, Sequoia, and Yosemite). The General Grant National Park was tiny—just under 1000 hectares (2,500 acres). It included the General Grant Tree, but only 84 hectares of giant sequoias within Grant Grove. Sequoia National Park was much larger, at 66,900 hectares (165,300 acres), and centered on a large concentration of sequoia groves just 15 kilometers south of Grant Grove. At Yosemite, the two small parcels of the 1864 land grant were greatly expanded into a formal national park on the scale of Yellowstone, which had previously been established as the first national park in 1872.

Logging the Giant Sequoias

Grant Grove is surrounded by several other giant sequoia groves, including two of the very largest, but these were left out of the tiny General Grant National Park. Logging interests pounced on the opportunity and acquired more than 12,000 hectares of prime forest through loopholes in the public land laws of the 1880s. As a result, several giant sequoia groves were logged during a 30-year period starting in 1883. Thanks to the amazing efforts of photographer C.C. Curtis, who—burdened with a 45-pound camera and glass plate negatives—recorded much of this logging history in great detail.

Just a few kilometers south of Grant Grove is the **Big Stump Grove**, so called because it has been completely logged. However, it is noteworthy in our story of champion trees for two of its impressive stumps. **Burnt Monarch** is now a 28-meter-tall snag and was

probably a snag before logging occurred. Even though the sapwood and bark are missing (and the bark of a giant sequoia can be up to 78 centimeters thick—thicker than any other tree in the world), the remaining portion is still larger than lower portion of the largest trees alive today. As such, it is one of only two known examples of a giant sequoia that may have been larger by volume than the **General Sherman Tree**, the largest living tree in the world. Since nothing is known about the upper part of this tree, however, the matter will never be resolved.

The **Mark Twain Tree** was one of the most perfect specimens of giant sequoia ever known, a fact that caused its demise. This tree, 700 centimeters in diameter and 90 meters tall, did not have any fire scars, so it was chosen to provide perfect giant sequoia cross-sections for museums. The felling of this tree in 1891 provided some of the most dramatic logging photos in history [Figure 5]. In the end, two sections were cut from the base, one of which was sent to the American Museum of Natural History in New York and the other to the British Museum in London. The remainder of the tree was cut into fenceposts and grape stakes; because wood from giant sequoia is extremely brittle, it has limited uses as lumber.

By far the most dramatic of logging episodes of the 1800s occurred in **Converse Basin Grove**. Located on a rolling plateau on the lip of Kings Canyon, it is among the largest of all groves (1,400 hectares with giant sequoias). That massive logging operation retains several world records, including the largest tree ever cut down by humans, a 59-mile-long lumber flume that stretched into the Central Valley, and four of the eight known sequoia trees that have been verified to be over 3,000 years old.

Figure 5. An 1891 photo taken during the early portion of the eight-day felling of the Mark Twain Tree. Insets show the only remaining pieces. [C.C. Curtis, *California History Section Picture Catalog*; California State Library. Inset photos: Wikimedia]





Figure 6. An 1892 photo of workers dismantling the General Noble Tree to create a two-story building for the 1893 World Columbia Exhibition. [C.C. Curtis, California History Section Picture Catalog: California State Library.]

A year after the felling of the Mark Twain, news spread of a spectacular fair coming to Chicago commemorating the 400th anniversary of Columbus' famous voyage. Due to criticism of earlier displays of giant sequoia using only the bark, the exhibitors decided to construct a two-story building, complete with cross sections of the trees, so there could be no question of the legitimacy of the display. They selected the **General Noble Tree** in Converse Basin Grove to be the tree displayed at the fair. If alive today, the General Noble would probably rank among the top 10 largest trees in the world [Figure 6]. More than 700,000 people visited the 1893 World's Columbian Exposition in Chicago, making it the most attended public event in history to that point, and the General Noble was a big attraction. After the fair, the reassembled tree went on display on the National Mall in Washington DC, where it remained until it was removed in 1932.

In 1919, A.E. Douglass (grandfather of tree-ring research) and several associates entered the logged grove to examine some of the stumps. They deter-

mined that the former General Noble, by then renamed the **Chicago Stump**, to have been more than 3,000 years old when cut.

Legend has it that Frank Boole, who ran the Converse Basin logging operation, spared the largest tree in the grove. Now named the **Boole Tree**, it grows near the lip of Kings Canyon among younger trees that have grown up since logging days. The Boole does indeed have a tremendously large base and is currently the sixth largest known giant sequoia, but we will never know whether it was larger than General Noble.

The Titans of Giant Forest

In 1858, Hale Tharp became the first Euro-American to enter **Giant Forest**—the crown jewel of Sequoia National Park. He lived in a hollowed-out log and raised cattle in nearby meadows from 1861 until the creation of the National Park in 1890. John Muir first visited Giant Forest in 1875 and wrote about meeting a fellow there who had several horses and was living in a giant log. We don't know if either Tharp or Muir knew about the General Sherman Tree at that time.

The **General Sherman Tree** in Giant Forest—first documented and named in 1879 by James Wolverton—is currently recognized as the largest living tree in the world at 830 centimeters in diameter, 83.6 meters tall, and with a volume of 1,453 m³. A small group of socialists called the Kaweah Colony were also aware of the tree and renamed it for Karl Marx. They spent several years building a road up to Giant Forest from the Central Valley but were unable to complete this monumental task. The General Sherman name was restored upon creation of the National Park in 1890, and the road to Giant Forest that the socialists had begun was finally completed in 1903.

We now know that half of the 14 largest trees on Earth grow in Giant Forest, including four of the top five. In 1976 one of those trees, the **Washington Tree**, was accurately measured as the second largest tree in the world by volume (1,360 m³) followed closely by the General Grant (1,321 m³).

No formal measurements of the Giant Forest trees, including wood volume, were made during the early 20th century, so many people considered the General Grant to be the largest tree due to its incredibly large base. Unlike most of the really large trees, which have spike tops extending above the live crowns due to lightning strikes, Grant appears—from the main viewpoint—to have an intact top. This is actually an illusion: An upward-tending side branch obscures the actual top, which is a dead spike. Even so, the crown has a very pleasing form, nicely offset by the interesting texture of the trunk. On

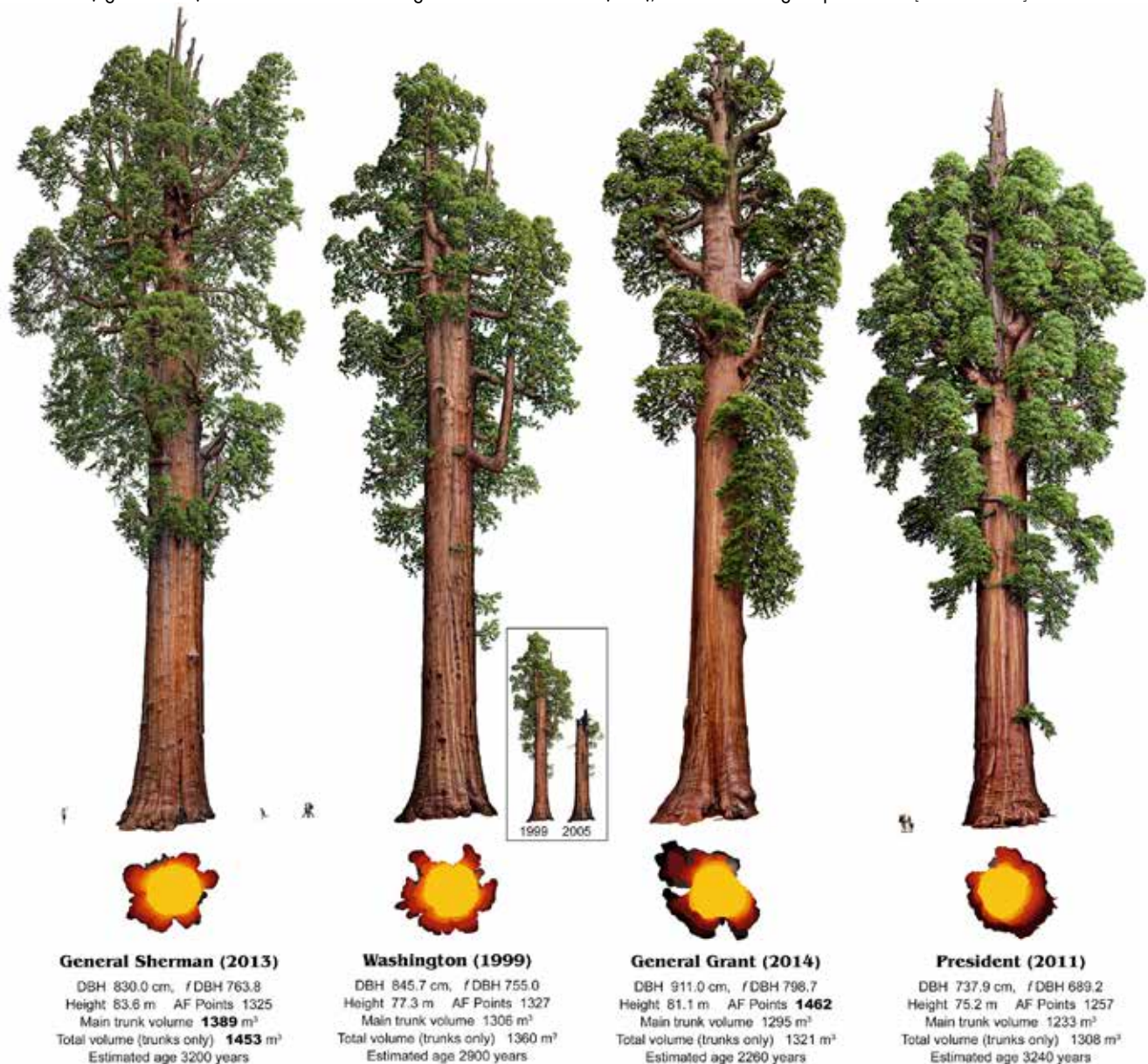
Christmas Day of 1925, with great ceremony, the General Grant was officially christened the National Christmas Tree by presidential decree. Annual events have taken place at the tree every Christmas since.

Objective measurements to determine which was the largest tree in Giant Forest began in the late 1920s. The Great Tulare-Fresno Contest started as a friendly rivalry between Tulare and Fresno counties, where General Grant and Sequoia National Parks were located. The Chambers of Commerce of the two counties sponsored a team of engineers headed by surveyor J.W. Jourdan to settle the dispute. Two trees from each county were selected for the contest. Fresno nominated the General Grant and Boole trees. Tulare nomi-

nated the General Sherman and the **Hart**, a large tree in the **Redwood Mountain Grove**, at that time the largest unlogged yet unprotected grove, which had the highest density of large giant sequoia.

By 1931 the team had made detailed measurements of all four trees. They used volume as the standard to compare the trees, and the results showed that the General Sherman was the largest, followed in order by General Grant, Boole, and Hart. The care and accuracy of the Jourdan team's measurements was evidently sufficient to calm any controversy, though lingering questions remained about the status of several other trees in Giant Forest, which were considerably larger than the Hart.

Figure 7. Orthographic paintings of the Earth's four largest trees as of 2000, and their date of most recent measurement. Inset shows that Washington lost its crown following a lightning fire and is no longer 2nd largest. Views are orthographic (undistorted) so will look different from photographs taken from similar viewpoint. Tree basal *footprints* show cross-sections of the trees from ground level (darkest color) to 18 meters (lightest color). While Sherman is the largest in terms of volume (bold), Grant has a higher point total. [Robert Van Pelt]



Into the Modern Era

Most of the credit for our current state of knowledge on the largest giant sequoias goes to Wendell Flint, author of *To Find the Biggest Tree* (1987). Flint was a retired mathematics teacher who spent nearly 50 years researching and measuring the volumes of the largest giant sequoias. His book summarizes current (and past) records of giant sequoia sizes.

Most recently, I participated in additional studies of the very largest trees. We created detailed 3-D models of the bases of the four largest trees, which entailed doing detailed surveys of trunk taper. And we conducted hyper-detailed laser scans of the trunks and crowns of the General Sherman and the **President** (also in Giant Forest) trees. Climbers scaled the Washington and the President to get direct measurements of trunk taper. Taken altogether, this information provides the most accurate statistics for these four trees [Figure 7].

III. Sugar Pine: Back to Calaveras

The third featured species is sugar pine, which takes us back to the Calaveras area. Ever since news of the Discovery Grove reached the world during the 1850s, timbermen were attracted to the area. We now realize that the Calaveras area had the largest and densest pine forests on Earth. Conservationists (including John Muir) became concerned that both giant sequoia and associated pine forests would soon be lost to logging, so they sent petitions to the federal government, and in 1909 President Teddy Roosevelt signed a decree to preserve the Discovery Grove and some of the surrounding pine forests. However, lumberman Robert Whiteside initially refused to sell his parcels that included Discovery Grove and the land remained unprotected until the creation of Calaveras Big Trees State Park in 1931.

Outside of the small Discovery Grove, sugar pine was the real king of these forests. Unfortunately, logging of these pines between 1852 and 1931 was so extensive that we will never be fully knowledgeable about what was once there. The first photographic record of a giant pine from the Calaveras area was a tree known to John Muir, who was photographed with it in 1900 [Figure 8].

This tree was first officially recognized as the largest sugar pine when it was measured in 1937, after the land had been purchased by the Girl Scouts of Northern California. They eventually named the tree after Maude Whelan, a major benefactor of the Girl Scout camp. The tree was featured in the very first National Register, listed at 306 centimeters in diame-

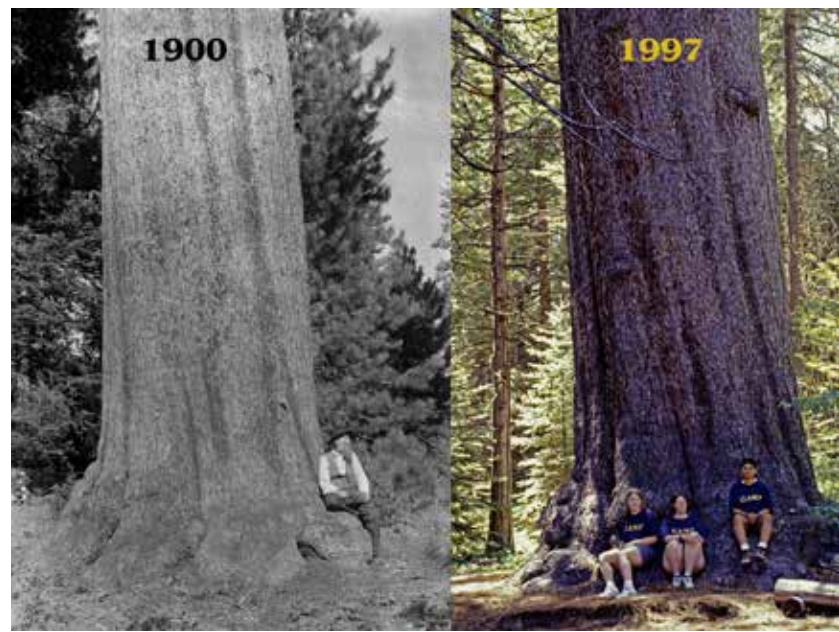


Figure 8. The largest pine ever recorded has always been this tree – shown here with John Muir in 1900 and with some campers in 1997. The property was purchased by the Girl Scouts in 1937, and the tree thrived until 2010, when it was attacked by bark beetles and died a couple years later. [1900 Muir photo: C.H. Merriam, Holt-Atherton Special Collections, University of the Pacific Library. 1997 photo: Robert Van Pelt]

ter and 61 meters tall. It remained the champion sugar pine until 1972 when a larger tree was discovered growing just six kilometers away in Stanislaus Canyon, on land owned by the Pickering Lumber Company. This tree, the **Pickering Pine**, measured 310 centimeters in diameter and 65.8 meters tall, giving it enough AF points to become the new champion. While the tree supported a large and healthy crown, two large fire scars adorned its base, one of which extended right through the trunk to the other side.

By 2000, when the largest sugar pines were accurately measured for volume, Pickering Pine was actually found to be smaller than the **Whelan Tree**, despite the larger basal diameter. By then two other large sugar pines had been discovered in the vicinity [Figure 9]. Sadly, all four of these giant pines are now dead—two from bark beetles, and the other two from rot in the base. Not surprisingly, the largest known living sugar pine is also located in this same area, which is in the heart of **South Calaveras Grove** of Calaveras Big Trees State Park.

The *tallest* known sugar pine of the 20th century grew near a wet meadow in Yosemite National Park. First recognized in 1991, the towering 81.7 meter tall tree was a rare example in which the tallest tree was also among the largest. It was the most perfect specimen I have ever seen, but bark beetles are the Achilles' heel of sugar pines: They attacked and killed this beauty in 2007 [Figure 10].

IV. Many, Many Ponderosa Pines

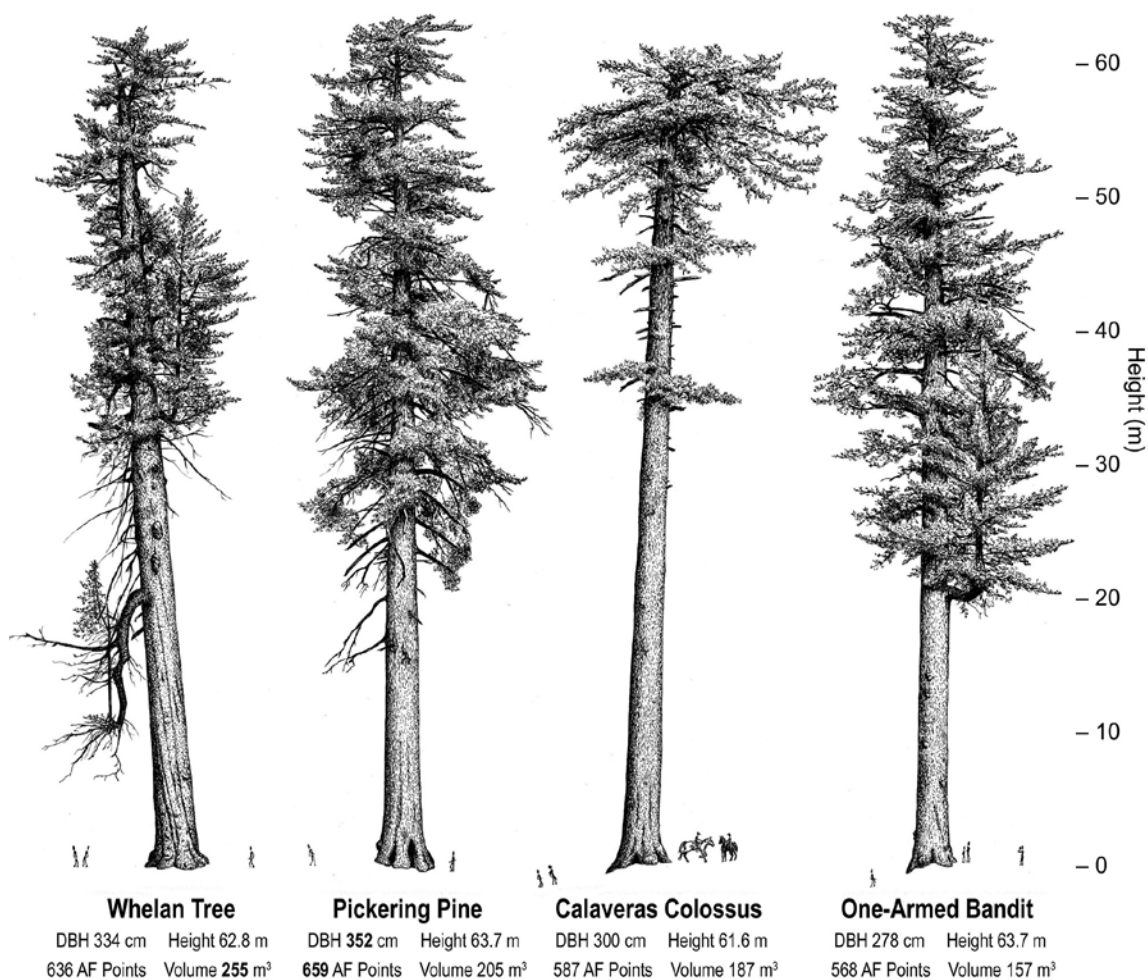
Our fourth species is the ponderosa pine, an extremely widespread and variable species. *American Forests* initially listed a single champion ponderosa, but there are now four types of ponderosa pine listed for champion status: var. *ponderosa*, which is found in Idaho, eastern Washington and Oregon; var. *scopulorum*, which occupies the northern Rocky Mountains to southern Colorado; var. *brachytera*, which occurs largely in Arizona and New Mexico; and the tall-growing Pacific variety *benthamiana*, which grows in southwest Oregon and throughout California.

Below: Figure 9. Illustrations of the four largest known sugar pines as of 2000, which were all located within 9 kilometers of each other in and around Calaveras. All four are now dead. [Robert Van Pelt, *Forest Giants of the Pacific Coast* (2001).]

Right: Figure 10. Tallest known sugar pine of the 20th century grew near a wet meadow in Yosemite National Park. First recognized in 1991, it was one of the few examples in which the tallest tree was also among the largest. It was attacked and killed by bark beetles in 2007. [Robert Van Pelt]



World's largest pines - 2000



The tree listed on the first National Register was near Mount Adams in Washington, but was replaced in 1943 by a larger tree near La Pine, Oregon, which measured 263 centimeters in diameter. The La Pine Giant retains the distinction of the largest diameter for the species, but lost its big tree champion status in 1969, when the first of several larger Pacific ponderosas were discovered. However, when *American Forests* separated out the Pacific ponderosa var. *benthamiana* as a separate category in 2012, the La Pine Giant regained its champion status for var. *ponderosa*. It's never easy being at the top!

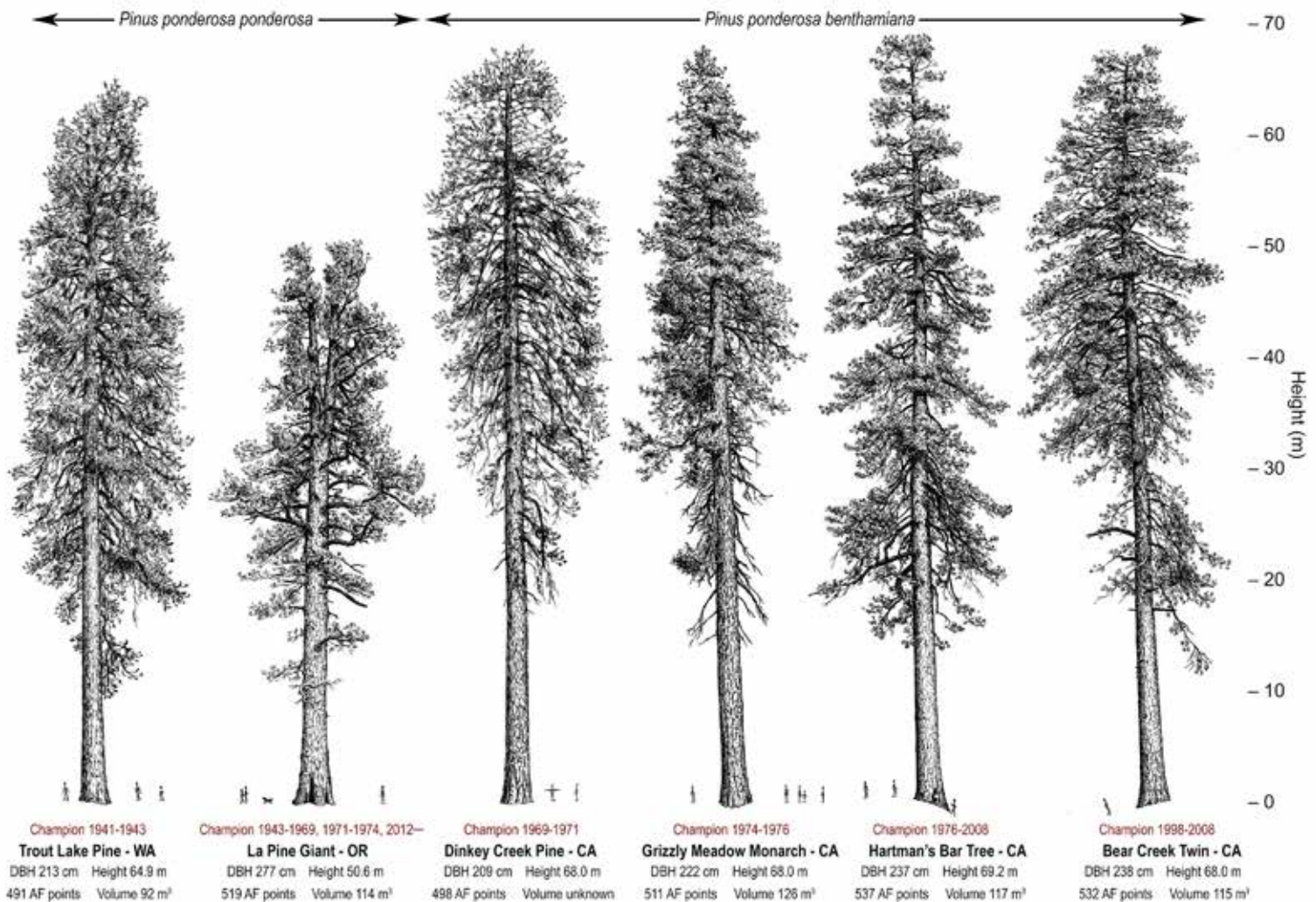
In the mid-1990s, with Wendell Flint's legacy as inspiration and his techniques as guide, I began measuring many species of giant trees for volume. I had long recognized that the point system used by *American Forests* was a useful approach to identifying the largest, but it breaks down with really big trees due to the dis-

proportionate influence that circumference plays in the AF Point total.

By 2000, I had measured more than a dozen giant ponderosa pines in an effort to identify the five largest by volume, as there were so many trees of similar proportions. Fortunately, a couple of former champions were still alive, including the largest by volume, which was briefly the National Champion in 1974. **Grizzly Meadow Monarch** is found just south of Yosemite National Park, and has a modest diameter of 222 centimeters, which allowed other large pines to out-point it. However, the Monarch has a very low rate of taper, and from 16 meters above ground to the top this tree had a larger diameter and thus more wood volume (126 meters³) than its rivals. In 1976, the **Hartman's Bar Tree** was discovered deep in the canyon of the Middle Fork Feather River in Plumas National Forest and its larger diameter qualified it as the new champion. [Figure 11]

Figure 11. Progressive list of national champion ponderosa pines to 2008. I was able to visit and measure the volume of all these trees but one, whose illustration was achieved with help of photographs and measurements by others. If nothing else, these trees illustrate that DBH, AF points, and size are related but very different. [Robert Van Pelt, Forest Giants of the Pacific Coast (2001).]

Progressive list of national champion ponderosa pines 1941-2008



In 1998, I met retired Forest Service District Ranger Al Gronki who showed me another giant ponderosa in the Trinity Alps Wilderness. We named it the **Bear Creek Twin** because a very similar tree grew only a few meters away, and the two trees together formed an imposing spectacle. It might as well be called Hartman's Bar Twin, because the diameter, height, and volume were nearly identical to the Hartman's Bar Tree. Al and I nominated the Bear Creek tree, and the two trees shared Pacific ponderosa pine champion status for the next 10 years.

All this complex history of changing champion tree status and volume versus AF points became moot in 2008 when foresters from the El Dorado National Forest found a new tree surpassing all others, regardless of method of comparison. When I visited to measure it in 2011, my first view from a distance gave the impression that the tree was young—branch structure and crown form were quite simple compared to champions I had measured previously. Only when I was standing at the base did it sink in that this tree was truly in a class by itself—considerably larger than all previous champions, at 576 points and 153 m³ [Figure 12].

WHY WE CARE

Trees touch all of humanity—every culture, spanning the centuries, back to the depths of time. Trees are one of the few living things on Earth that can dwarf humans with their extreme size and age. They appear in central roles in many of the world's mythologies and religions as representations of eternal life or fertility—as keepers of the past and a promise of the future. Similarly, their size and structure features prominently in many cultures as a symbol of strength and inspiration, and trees were often a framework cultures used to explain their universe—The Tree of Life mythology (in some form) is found in most cultures. Certain giant conifers are still considered sacred in Taiwan, Japan, and Mexico. Here in the U.S., we've created dozens of state parks and several national parks specifically to protect the ancient trees growing there.

Does size matter? For the ecologist and botanist, large trees indicate both an excellent adaptation of the individual tree to the conditions of a given environment, and to the health and potential of that particular

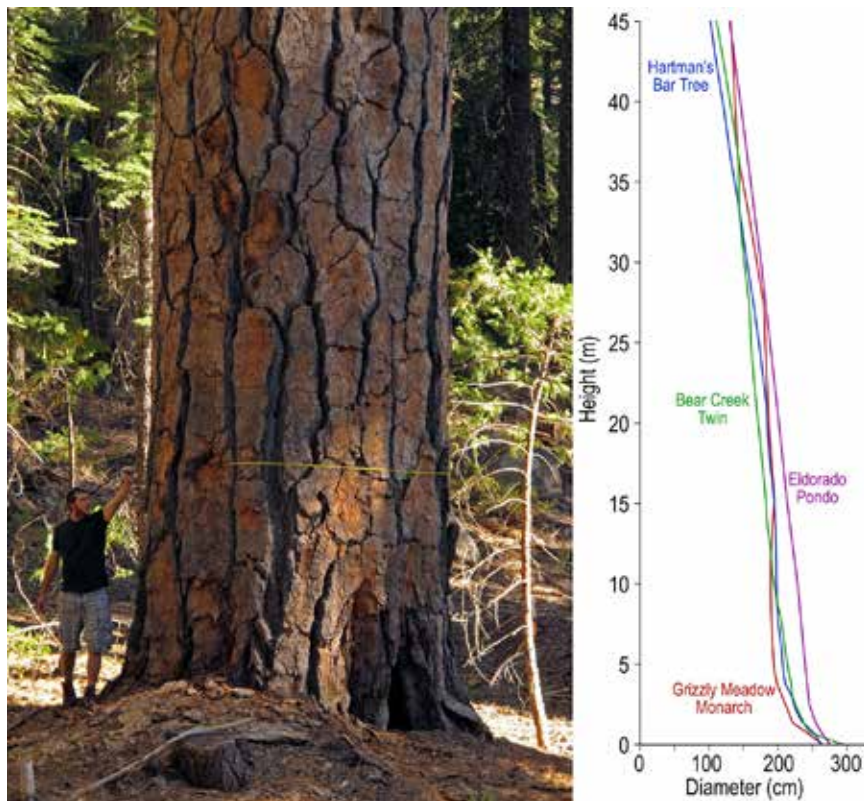


Figure 12. Largest ponderosa pine ever recorded was discovered in 2008 by foresters of El Dorado National Forest in the central Sierra. Left: Man is shown stretching the 2-meter tape wrap, and the extremely slow taper is obvious. Oddly, the bark and branch characteristics of this tree suggest it is younger than all preceding champions. [Robert Van Pelt] Right: Taper characteristics of current and previous champion *P. benthamiana*.

location. For the layperson, extreme size is a source of awe and therefore a way into an appreciation of both the trees and their habitats and—we can hope—support for their ongoing protection and stewardship.

As someone who is dedicated to observing, documenting, and quantifying these arboreal wonders, I realize that humanity still has much to learn from giant trees, and these trees still have much to teach us.

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A ONCE AND FUTURE FOREST:

AN INTERVIEW WITH EMILY BURNS OF SAVE THE REDWOODS LEAGUE

California is home to the largest trees in the world. And none are larger, or more iconic, than the two species of redwood—*Sequoia sempervirens* (coast redwood) and *Sequoiadendron giganteum* (giant sequoia)—that grow here and nowhere else (except a small sliver of Oregon). In many ways, the long battle to save these trees has also been iconic, an emblem of the state's long and proud tradition of conservation.

And speaking of long and proud conservation traditions, last year, Save the Redwoods League celebrated its centennial as an organization dedicated to protecting, and educating the public about, the redwoods. To mark this milestone, the venerable San Francisco-based nonprofit published two important documents. The *State of Redwoods Conservation Report* is a comprehensive look at the status of these two species after 100 years of both intensive logging and dogged conservation. Then looking forward, *Centennial Vision for Redwoods Conservation* sets out both an inspiring long-term strategy and a set of ambitious medium-term goals for nurturing the redwood forests of the future. (Both publications are available for free download at savetheredwoods.org.)

One of the authors of these reports is Emily Burns, Director of Science for Save the Redwoods League from 2010 to 2019. In that role, Burns ensured that all the League's conservation, stewardship, and advocacy programs are grounded in science. She directed the League's Research Program, and in particular the Redwoods and Climate Change Initiative, the Redwood Genome Project, and the Vibrant Forests Plan. In May 2019, Burns will leave the League to become Program Director at the Sky Island Alliance in Tucson.

Burns sat down with *Fremontia* guest editor David Loeb on a rainy winter day to discuss the current state of redwood forests and her hopes for their future.

Q – How did you first get interested in redwood trees?

A – I grew up in San Rafael under redwoods my parents had planted in the yard of their house. But my professional interest in redwoods started in the early 2000s, when I heard a lecture by Professor Todd Dawson at UC Berkeley about how redwood trees are able to absorb fog water directly into their leaves, and it blew my mind. I had just graduated from UC Davis with a degree in plant biology, but had never heard

anything about this phenomenon that we call foliar uptake. And it made me realize that there is so much about these remarkable trees that we don't know, so I decided to go to graduate school to study this particular phenomenon. I went to UC Berkeley to study with Todd and in my research learned that about 80% of the plants in the redwood forest can do foliar uptake.

This grove in Humboldt Redwoods State Park features widely-spaced old-growth trees interspersed with a mix of younger trees. [Max Foster]

Was this not known before you started studying it?

For species in the redwood forest, foliar uptake had only been documented in redwoods. I surveyed other trees and shrubs, herbaceous plants like redwood sorrel, ferns, and I found that it's actually western sword fern that that does the most foliar uptake—absorbing about twice as much moisture as redwoods [per unit leaf area]. My research started focusing on the ferns, and I got to know Save the Redwoods League because it helped fund my research. When the job of science director at the League came open in 2010, it really spoke to me because, while I love basic research, I saw the importance of being able to apply research to decisions on the ground, to conservation.



Emily Burns started her career in redwoods by studying the significant role of foliar uptake by western sword ferns in the redwood forest ecosystem. [Joan Hamilton]

Let's start with a few questions about the League's new State of the Redwoods report. What portion of California's remaining redwood forest is old-growth?

We have 1.6 million acres of redwood forest in the state today, compared with 2.2 million acres before the Gold Rush, so we've lost about a quarter of the redwood forest overall, due to logging and conversion. Of the remaining forest, about 7%—113,000 acres—is considered old-growth.

What percentage of that old-growth forest is protected?

About 90,000 acres of old-growth forest is protected through a combination of public ownership, conservation easement, or nonprofit ownership with conservation intent.

Looking at all types of redwood forest, what percentage is protected?

Protected forest, meaning no logging or development allowed, covers 22%, or 345,000 acres. But there's another 200,000 acres of what we would call partially protected, where some rights are restricted, with limited logging or development allowed. Conservation is a range, with many different flavors. But that 22% has the highest level of protection.

Going beyond protection, there's the question of the health of the forest. What did you find in comparing the health of the redwood forest today versus the health of the forest 100 years ago.

Over the last century, there's been a race between protecting land and very aggressive commercial logging

and conversion. The redwood forest 100 years ago had many more contiguous patches of old-growth redwood forest, but at the same time, much less of the forest was protected. While we've had a blossoming of redwood parks, we've also seen the landscape of old-growth be largely reset into a very different type of forest, due to clear-cutting. Today we have islands of old growth surrounded by a sea of forests of different ages. The oldest second growth that we have was cut in the Gold Rush era, so it's now about 170 years old. It's actually rare to find this kind of mature second growth, and it has recovered many, but not all, of the important ecological traits of old growth—tree size, density of trees—and is beginning to resemble old growth.

These forests didn't suffer from the same sort of aggressive logging that we had later, like in the 1960s, when tractor logging decimated redwood watersheds and scarred them with logging roads, and the subsequent high-density restocking with Douglas-fir changed the forests by displacing the historically dominant redwoods.

Does a forest replanted in Douglas-fir have potential for recovery?

It does. The resilience is captured in the name, *Sequoia sempervirens*—always green, always living—the trees have this amazing ability to tolerate shady conditions. You can cut them down to the ground and they resprout. But where they have high density of Douglas-fir around them, they may not be able to proliferate without help, and they're not going to become canopy dominant as easily.



Top: Relictual old-growth redwood groves stand out as islands in a sea of formerly-logged forest in Redwood National and State Parks, Humboldt County. [Mike Shoys] Above: Aerial view of industrial timberland with recent clearcuts, right next to Redwood National Park (in upper right corner). Note the narrow state-required riparian buffers between some of the clearcuts and the overall fragmentation due to logging roads. [USDA Farm Service Agency]

Were there any findings from the report that particularly surprised you?

Yes, there were a couple. I was surprised that over half the redwood forest today is in the category of youngest, smallest stature forest. That just gives a sense of the scale of the restoration work ahead of us. These are forests that have lost their large old trees, they have lost their carbon storage, they've lost their wildlife habitat value. So they have dramatically changed.

And then for me, the other surprising piece was about the impact of the network of roads—both logging and residential roads—that have divided and carved up so much of the redwood forest. It's not a contiguous 1.6 million acres of redwood forest. There are many hundreds of abandoned logging roads that have unstable sediment that threaten salmon-bearing

streams. We calculate that more than a quarter of the redwood forest today—400,000 acres—is impacted by these roads.

So we can't just say we have this much mature forest. The size of the patches matters.

Yes, even for what we think of as our best protected redwood areas, we have the "Redwood Highway" running through them. Of course these parks were created intentionally because they were easily accessible for visitors, and that's still important today. We need roads and we need infrastructure to take care of the forest. We need people to go to and love the redwood forest, but roads do have a natural resource impact. We are trying to figure out which are the nonessential roads, which roads we don't need any more and can remove.

Another element in the report that was surprising to me was the claim that redwoods have the greatest capacity for storing carbon of any forest type, per acre.

That finding came from our Redwoods and Climate Change Initiative that started in 2009 and that established 16 one-hectare inventory plots scattered throughout the redwood region in collaboration with a team led by Stephen Sillett at Humboldt State. All of the aboveground biomass within these plots was inventoried and from that biomass, we can

estimate the stored carbon, which was record-breaking at the northern end of the range. For example, at Jedediah Smith State Park, which is in the California temperate rainforest, we have more than 5,000 metric tons of biomass per hectare, which translates to about 1,000 tons of carbon per acre.

How do you determine the amount of carbon storage?

The team takes core samples and partitions the biomass to see how much is bark, how much is sapwood, how much is heartwood, and estimates carbon within each category. The heartwood is the most important reservoir of carbon. I consider it a carbon sink. Many forests are accused of losing carbon back to the atmosphere, but redwood heartwood is the best at holding on to carbon for many millennia, because it's decay and pest resistant. Redwoods in older forests have had more time to accumulate heartwood, and the combination of the living and dead trees make up the totality of that biomass. Whereas a young forest is accumulating wood quickly, but the trees are so small, even though

the rate of growth is fast, they don't have many leaves and only a small growing surface to build wood. The ability of young redwoods to sequester and store carbon is just a fraction of what an old tree can do. The younger forests that are recovering will catch up, but it's going to take generations to reaccumulate that biomass.

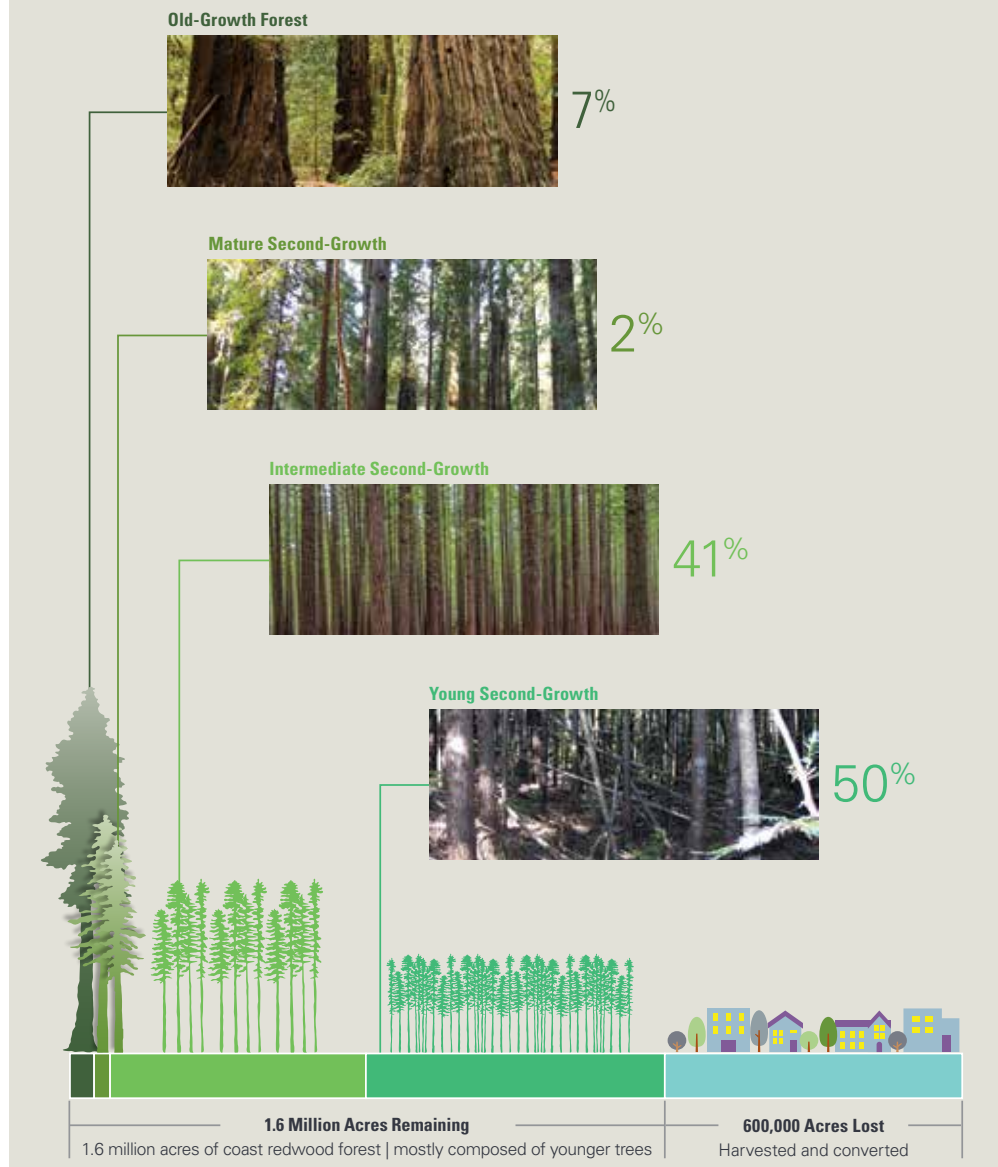
I read that growth in these old trees is surprisingly fast. That they don't stop growing when they get old, like we do.

Oh right, the fastest growing redwood trees are old and large, unlike people, where we taper off and then start to shrink; that doesn't happen in redwoods; they continue to grow. As a continuation of our research we've been looking at wood production rates in redwoods all over the state. It's remarkable, old redwood trees are growing faster now than they ever have in their lifetimes, even during the drought that we just had. We've seen this growth surge, especially since the 1970s, which is pretty remarkable.

So do we know what the impact of climate change has been on the forest?

There's a couple of ways to answer that. One is looking at these growth trends in coast redwoods. In old growth we've seen a distinct increase in wood production starting in the 1970s. Why is that? Lots of factors probably. As the climate has been warming, carbon dioxide levels have been going up, which simply provides trees more carbon to fix through photosynthesis. Interestingly, on the coast we've seen a reduction in summertime fog and cloudiness, as well as less particulate pollution and improvement in air quality as the timber industry stopped using teepee burners. We can't say which one of those factors is better able to explain what we're seeing, but the trees have had more sunlight and we see a very clear and distinct growth response. If redwood trees have enough water and light, their growth rates are unstoppable.

THE LEGACY OF LOGGING



The fact that over 90% of the state's remaining redwood forests are composed of young trees means that restoring old-growth features to these forests will be the work of many generations.

[Save the Redwoods League, 2018]

The other way we look at climate change impacts is to compare different redwood forests because they span a really large climate gradient along the coast, with twice as much rainfall up north as in the southern part of the range. It's sort of a proxy for climate change because we can ask, how do redwood forests grow when they have only half the rainfall and warmer summers? We find more of the drought signal in forests in the south, that are typically dryer and warmer. It may be that these forests have experienced more frequent fire, and when they do burn, the trees have to invest in healing themselves, and this prevents them from having the kind of growth acceleration that you see when they're uninjured and have



Healthy streams in old-growth redwood forests, such as seen here at Montgomery Woods Redwoods State Park in Mendocino County [Ken Van Der Wende], provide critical habitat for coho salmon (above) and other native species. [NOAA Fisheries]

lots of resources—like lots of water, lots of growing space. Fire frequency is definitely coupled with climate change, so I think that is one aspect of redwood forest ecology that we need to track closely in the future.

Okay, let's move now to the Centennial Vision report, which lays out a pretty ambitious goal of creating the old-growth forests of the future, with a shifted emphasis from protection to restoration.

We realize that our protection work is not over; there is more forest to protect and there's a need to create a more connected, larger redwood reserve system. But a lot of the remaining old growth has been protected, so the protection work is going to be happening hand-in-hand with restoration, and with long-term sustaining stewardship. And because most of the currently unpro-

tected forests have been logged in the past, we are looking for the critical places where restoration is needed to put those forests on the best recovery trajectory.

This is where the terminology gets funny. Redwood forests that have been logged need to **recover**. They don't all need **restoration**, which is an intentional intervention. I like to say that a doctor wants all of her patients to recover, but they don't all need surgery. So when we think about the restoration vision, it really is about the broader sense of the recovery of redwood forests and we don't want there to be just 113,000 acres of old growth. We want there to be at least 800,000 acres of old growth—many generations from now.

Can you explain the concept of old-growth forest structure, which is talked about in the Centennial Vision?

We can't run the clock forward and make the trees grow old quickly. But what we can do is help them increase their growth potential to get large as quickly as possible. One of the elements of old-growth structure that we're trying to recover in logged forests is greater space between trees—reducing the number of trees per acre. If you walk through an old-growth redwood forest you can see between these large columns of trees. There are still small trees in a healthy old-growth forest but most of the biomass is accumulated on individual large trees. A forest recovering naturally, if it was a young redwood forest, not a planted Douglas-fir forest, would self-select through natural competition among young redwood trees. Eventually, emergent redwoods would become the upper part of the canopy, occupy the space, and really build out their biomass over time. When we thin the forest and reduce

the density in a young redwood forest, it creates space and additional light that stimulates a growth-release in the redwoods left behind.

In an old-growth forest, we see many elements of complexity that developed over centuries—open patches where more light is getting down to the forest floor; snags—dead standing trees—that are really important for wildlife habitat because birds build nests in the decaying trunks. And when these trunks fall to the ground they become nurse logs, habitat for many animals on the forest floor. So we're really looking for those elements of big trees, widely spaced trees, standing dead snags, wood on the ground, because when those elements are present the biodiversity increases. We see many more types of understory herbaceous plants and shrubs coming in. One of the things that people don't realize about the youngest redwood forests is that they're so dense that little else can grow. They're the darkest forests I've ever been in. The trees are all standing so close together, and they're certainly not letting any light down to the forest floor. But when you get in an old-growth forest, it's much more open, and it's that light that fuels productivity and biodiversity.

So scientists, like you, have learned how to nudge the forest along—how to give it a hand. Is that an active area of work at this point?

Well, yes, we have our project called Redwoods Rising, in Redwood National and State Parks. When that forest was clearcut, probably in the 1950s, they aerially re-seeded portions of it with Douglas-fir seeds from who knows where. *National Geographic* has photos of helicopter pilots in aviator glasses dumping out huge barrels of Douglas-fir—and redwood—seeds that were silver, because they were coated in rodenticide! Their goal was to reblanket the slopes, and they did. Now in collaboration with the parks we need to go in and figure out how to help the native coast redwoods reemerge and become dominant again. It does mean removing Douglas-firs—we're talking about cutting trees here—taking those trees out to reduce the density and at the same time removing the old crumbling logging roads. There are 70,000 acres of logged redwood forest within that park complex that surround the largest patches of old-growth on the planet. So we have a really exciting opportunity to help connect those old-growth islands once again by repairing and recovering the forest that's separating them.

This sounds like sort of a laboratory for the science of redwood forest recovery.

Yes, Redwoods Rising is symbolic of the League's centennial restoration vision. We've sponsored research into the efficacy of these treatments in that geography and other places in the redwood forest range to understand what happens when you cut trees for restoration, what is effective, how much of the treatment to do, because we don't want to remove any more trees than we need to. We're thinking about how to reduce the fire risk in these heavily stocked forests and we're thinking about how we can help create interim habitats for species that can only live in old growth.

Of course, we're going to need ongoing monitoring where we're doing forest management and to ask ourselves if we're seeing the outcomes that we expect. Have we reduced density? Are we increasing growth rates? Is redwood becoming dominant again? Are we protecting the native genetic diversity in these stands? Are we improving habitat quality? And did we stabilize sediment in these watersheds by doing the road removal?

What's driving us today is not trying to return everything to what it was in the past, but rather to create a forest that can be robust and vigorous despite the onslaught of future environmental changes. Research has shown that larger redwood trees that are spaced apart not only hold more carbon and are better for wildlife, they're also less likely to burn and more likely to have greater resilience to fire. Luckily all of these goals align in trying to return old-growth characteristics to our forests.



Forest ecologists Robert Van Pelt (University of Washington) and Laura Lalemand (Save the Redwoods League) survey the progress of habitat recovery on a previously logged plot near the town of Mendocino, as part of the League's Redwoods and Climate Change Initiative. [Andrew Slack]

Restoring this old-growth forest is going to require more than just recovering the trees. There are all these other organisms—from microbes to fungi to plants—that comprise an old-growth ecosystem. How will these come back? Are they latent, lying dormant in the forest?

That's one thing we're studying now: how readily native species can reoccupy recovering forests. I can give you a scientific answer, but I want to start with a personal one. In the Mill Creek watershed in Del Norte Redwoods State Park, which is one of the core areas for Redwoods Rising and one of our longest-running restoration projects, working with California State Parks. And it's one of the largest salmon strongholds in California, but it was almost entirely clear-cut—some 25,000-acres prior to its acquisition into the park. I went out there with volunteers who were helping collect data; we were comparing which species grow on the forest floor of a logged area with one of the nearby patches of old growth that wasn't cut, called the Hamilton Grove. I walked away from the volunteers while they were collecting and I was looking around and I noticed a frond of *Polypodium scolieri*—leather leaf fern—coming down out of the canopy; it's one of those species that grows on big old redwoods. And it just made me realize, "Wow! Even in a very small patch of old growth the species are there!" That plant in particular, with its windblown spores, will be able to repopulate recovering forests, once we build the structure and help the smaller redwood trees get big and form platforms to hold epiphytes. So I think recovery is possible. If we find out that it isn't, well, then my successors might have to think about doing transplants, or how else to repopulate.

What about all the components that make up the soil of old-growth ecosystems, the networks of mycelliae, etc.

Soil is such a frontier! We barely understand what species are growing below ground. But given that we still have redwoods in the logged forests, the ancient root systems are still alive underground, and they're sprouting new trunks aboveground, so my hope is that the microbial communities are not decimated. They may be changed, but I hope they'll also come back as the forests grows back as a whole. We would sure love to know more about that.

What role does fire—as a tool—play in this restoration vision?

Fire was much more frequent, certainly over the last 10,000 years at least, and we know that Indian tribes were burning in the redwood region, often to maintain meadows. And many of the characteristics we associ-

ate with old-growth forest are probably a result of that frequent burning. So fire is thought of as an important component of redwood forest ecology. How often a coast redwood forest needs to burn though, we don't know. Unlike giant sequoias that need fire to release their seeds and for those seeds to get established on the ground, redwood reproduction isn't dependent on fire. Fire helps create a lot of habitat structure, when it burns into a redwood trunk and creates hollows. That's when the bats can go in, for instance. And those kinds of structures form from many frequent fires over time. And fire can be a way to reduce tree density, if smaller redwood trees, or trees of other species, are killed with relatively low intensity burning. Though trying to get the exact prescription of tree density removal through prescribed fire is nearly impossible. And there's more fire risk to redwoods now with Sudden Oak Death. We've seen redwood trees being more vulnerable and actually dying during medium intensity fires, if there's a lot of standing fuels associated with SOD mortality.

Fire management is always going to be unique to a place. In places where there's no road access or where it wouldn't be responsible to bring heavy equipment in to do mechanical thinning, fire could be a really good tool. There's been a lot of discussion, and as we work more with local tribes, I think more and more we'll be exploring fire as a tool, learning from their experience and history of using fire in the redwood forest.

What about logging—conservation logging—as a tool in restoration?

Well, to me, logging just means cutting trees. It depends on why it's being done. So there's a range of protection levels across the redwood forest range; there's a range of need and perspectives as to how logging, and any revenue that could come from selling trees, fits into good forest management. Save the Redwoods League in particular is focused on ecological outcomes and wants to make sure that every prescription and any treatment that's designed in a restoration program, is done without being driven by financial concerns. But for many private landowners, the question of how you fund a restoration project, or even a fuels reduction project, is a real one, and I'm aware that the commercial sale of some trees can enable good stewardship practices in the forest overall.

After we design our restoration prescription, if logs are commercial size, and we've deployed all the wood we need to meet our ecological goals, including leaving dead snags, building up the woody debris on the forest floor, putting logs back in to streams to help rebuild aquatic habitat—once these ecological needs are met,

we do need to deal with the extra biomass, because it could be a fuels risk if it's just left on the floor. If we've met all of our wood needs, and there are logs of a commercial size, then they can be sold to help offset the cost. But restoration, if it's done correctly, is not a money maker! The cost of removing hundreds of miles of roads, doing tree planting, doing the fuels work, bringing in prescribed fire, and repairing streams that have been decimated is so costly that we're willing, with the right checks and balances in place, to sell some restoration by-products. But it's never going to pay for the whole process, though I wish it would!

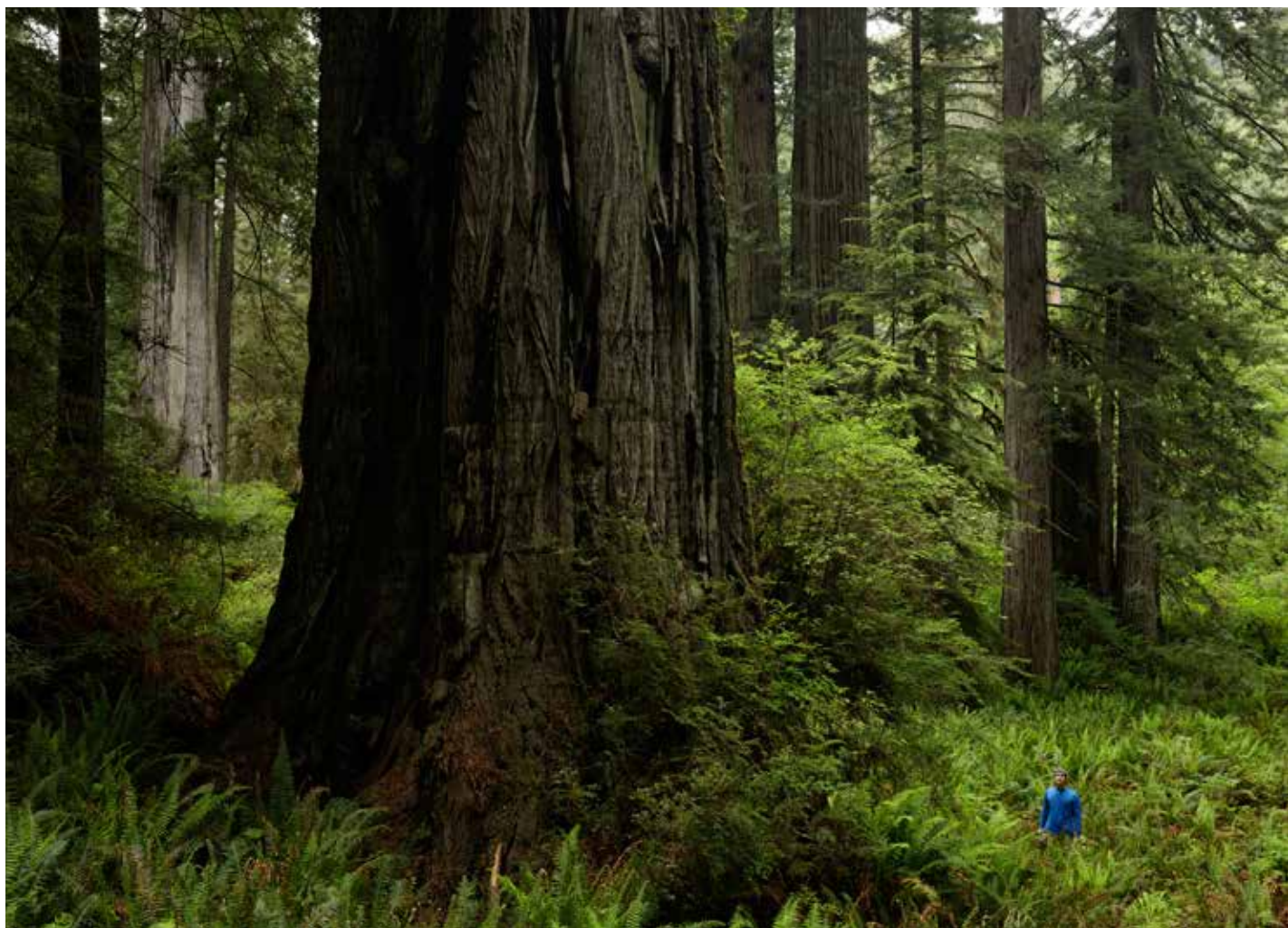
Will the redwood forests at the southern end of the range be able to survive the stresses of a warming planet?

I do think those coast redwoods are going to be able to tolerate change, and maybe even thrive, in their native range. But the structure of those trees, the pace at which they grow—those are all subject to change

as the environment around them evolves. Redwoods are so incredibly resilient—I look at tiny scraggly redwoods on the ridgetops along the Big Sur coast that burn all the time and they're still there! And they're setting seeds, they're sprouting back, and they're continuing to grow in a really harsh environment. But is that the kind of forest we think of at Muir Woods? Or up at Humboldt Redwoods State Park? No it's not; but the redwoods really are the backbone of these forests. So where you have redwood forests now, I feel confident that they will persist, at least for the rest of my lifetime, and continue to provide refuge for other species. And that's so important.

This Centennial Vision is such a massive undertaking: How will you mobilize the resources required? And what role can the public play?

Well, I think it requires a recommitment from the public and the private sector to protect and sustain our redwood forest. If I take Redwoods Rising as a



A hiker at Prairie Creek Redwoods State Park in Humboldt County is dwarfed by the old-growth redwoods. Increasing access to recreational opportunities in redwood parks is an important part of the League's Centennial Vision. [Max Foster]

discrete example... Since 1978, about 6,000 acres of forest restoration have happened within the Redwood National and State Park complex. By 2023, we're going to do at least another 5,000. So we were going to nearly double, in the first five years of this project, what happened over the last four decades. And to do that, it's being kickstarted with philanthropy, private individuals stepping up to invest in this recovery. And it's also building this movement, building new human resources, training the next generation of restoration professionals. We're bringing Humboldt State students into the parks, teaching them about restoration, building the workforce to do all this forest stewardship. And also inspiring the public with the vision of growing this forest back. It's so iconic for California; it's really a legacy project for all of California to be giving to future generations. At the same time we're investing in clean water for communities on the North Coast, we're building that global carbon reservoir, we're growing and sustaining populations of endangered species, and creating a remarkable place for people to go and visit. Getting people out into the forest is actually the third part—the "Connect" part—of the League's Centennial Vision, making redwood forests inviting and accessible to the people of California. The population is increasing, the diversity is increasing, and thinking about how to provide public access opportunities that both protect redwood forests and are welcoming to people who may see the forest really differently, means that we'll be doing a lot of investment in interpretation and education and public access, to provide a world-class park experience and help people form that bond with the redwood forest.

Could cap-and-trade funds provide support for this work?

There are several pools of state funding that have grant programs, like the greenhouse gas reduction fund.

Redwoods Rising is a great fit for that and we're inviting several state agencies to make investments in the project. Redwoods Rising was included in Governor Brown's budget last January. And the League, as it always has, is working to match with private money to help kickstart these efforts. So I think we're beginning to turn the tide in getting more public resources going into our public lands. This is critical, because we're not going to have the habitat needed for endangered species, or bring back those carbon storage reservoirs, if we wait. I think we've started a movement that will be successful long term, and we'll see significant progress in the short term. Every decade, from here on out, we'll be softening the edge between the old-growth islands and the sea of young forest around them. Every decade, we'll be hiding old growth back into the landscape, as the forest develops around it. Ten years from now, after an old logging road is removed, people may not know where it was, and the salmon habitat will return in these watersheds. The trees won't be incredibly tall, but they'll be larger, they'll be more spaced out, so I think we'll be able to walk into these forests and see measurable differences.

You've climbed into the redwood canopy numerous times. What's that like? And why would you ever want to come down?

Well, for one, the harness hurts when it's on for a long time! For me, everything about seeing the top of the redwood forest is fascinating, but what strikes me the most is how different the colors are, like the colors of the redwood leaves, when you're looking from the top down versus looking at them from underneath. They're actually really different, illuminated by the sunlight. You think of the redwood forest as being so shady, but that's just our perspective from down on the ground. Redwood forests get an incredible amount of sun. The trees are so remarkable because they've stood in the same location for centuries, withstanding all kinds of conditions—hail storms, lightning strikes, you name it, and so the fact that these trees are able to continue to thrive and grow faster now than they ever have, given that entire history through all the changes that California has seen, is pretty remarkable. You can't help but feel that you're perched in a being that is not only bigger than you are but certainly much more patient and adaptable. It is really humbling.

Emily Burns and a colleague ascend several hundred feet up an old-growth redwood in the Redwood Experimental Forest (near the Klamath River in Del Norte County) as part of a study of salamanders and other wildlife that live in the forest canopy. *[James Campbell-Spickler]*





PIUTE CYPRESS: AN INTRIGUING PAST AND UNCERTAIN FUTURE

Text and Photos by Jim A. Bartel

Piute cypress, named *Cupressus nevadensis* by LeRoy Abrams in 1919 for the Sierra Nevada, is one of three cypress species native to that mountain range. These Sierran species and the remaining New World or western cypresses were all placed in the newly described genus *Hesperocyparis* in 2009 (Adams et al. 2009). Apparently no more than late Miocene (6 mya) in age, this genus has diversified at a rate that is among the highest reported for gymnosperms (Terry et al. 2016).

While the Piute cypress (*Hesperocyparis nevadensis*) was long thought to be allied with smooth Arizona cypress (*H. glabra*) or Arizona cypress (*H. arizonica*), genetic studies have shown that the tree is most closely related to Sargent cypress (*H. sargentii*) and is also closely allied to four coastal species: Gowen cypress (*H. goveniana*), Mendocino cypress (*H. pygmaea*), Monterey cypress (*H. macrocarpa*), and Santa Cruz cypress (*H. abramsiana*) (Terry et al. 2012).

Among the native California cypresses, Piute cypress is easy to identify. Like its five closely allied species and MacNab cypress (*H. macnabiana*), mature Piute cypress trees have rough, fibrous, and often furrowed bark, as opposed to the smooth, generally exfoliating bark of Baker cypress (*H. bakeri*) and the two south-

ern California species, Cuyamaca cypress (*H. stephensonii*) and Tecate cypress (*H. forbesii*). Unlike the other fibrous barked cypresses, Piute and MacNab cypress have active leaf glands that exude a whitish resin. However, the small tree to shrub-like MacNab cypress has somewhat flattened ultimate branches that produce copious amounts of fragrant resin unlike Piute cypress.

Above: Six-year-old Piute cypress saplings, a few with a couple of immature cones, grow in the younger stand of the southeast portion of the Bodfish grove in 2017. Along with the burned cypress trees in the middle ground, cypress unaffected by the 2010 Canyon Fire can be seen in the distance above Myers Canyon, with Cook Peak much farther in the distance.

Below right: Rough, fibrous, and often-furrowed bark of mature Piute cypress trees. Below left: Close-up of branch tip of Piute cypress showing the whitish resin that accumulates from the exudation of the dorsal leaf pits.



Unrelated to the morphology of the Piute cypress and its relationship to other cypress species, there is now growing concern about its future health, given that increasing and repetitive wildfires appear to have reduced the size of some Piute cypress populations and may, in the future, reduce the number of its smaller populations. I discuss this concern below, as well as examine the natural history of Piute cypress, focusing on its interesting distribution and the complex geology underlying the populations, which may help explain their relative vulnerability to fire.

DISCOVERY AND USES

While the Sierra Nevada was used to give the species its scientific name, Piute cypress is endemic to only a small portion of that extensive range: the southern Sierra in the small ranges (including the “Piute Mountains”) surrounding Isabella Lake east of Bakersfield. Despite extensive development and heavy recreational use in the Isabella Lake area, the species receives little notice today from the vacationing public or local citizenry. In fact, the species was not discovered by American botanists until 1907, when Leo A. Herzinger, a school teacher from the town of Bodfish, sent specimens to William Dudley at Stanford University. “Miss Leo,”

as she was affectionately called by her students, taught for five years before marrying Alfred James Polkinghorne in 1912. After Dudley’s death in 1911, Mrs. Polkinghorne’s original and subsequent 1911 collections came to the attention of LeRoy Abrams, also at Stanford. After visiting the Bodfish grove in 1915 and collecting the type specimen, Abrams described the species four years later in the journal *Torreya*.



Carl Albert Purpus collecting California barrel cactus (*Ferocactus cylindraceus*) in the Colorado Desert of California. Image published in Walton’s *Cactus Journal* in 1899.

The first botanist, however, to recognize that a cypress grew in the Piute Mountains of Kern County was Carl Albert Purpus, a professional plant collector from Germany who specialized in searching remote areas of the American Southwest and adjoining Mexico, collecting unusual plants. The vagabond Purpus located several new taxa or range extensions in his travels

through the Piute Mountains in 1897, such as Kern County milkvetch (*Astragalus subvestitus*), rose-flowered larkspur (*Delphinium purpusii*), limestone dudleya (*Dudleya abramsii* subsp. *calcicola*), Nevada glossopetalon (*Glossopetalon spinescens* var. *aridum*), and Piute Mountains jewelflower (*Streptanthus cordatus* var. *piutensis*). Despite collecting seed from the Bodfish grove for introduction into Europe, Purpus thought the tree was merely a range extension of Arizona cypress.

Prior to Purpus’ 1897 exploration and to the botanical community’s recognition of Piute cypress as a distinct species, the tree may have been used for various purposes. Given the limited natural supply of timber in the southern Sierra south of the Kern River, gold and tungsten miners in the Clear Creek mining district may have used the wood for fence posts and shaft timbers as early as 1864, given the immediate proximity of the mines to the O’Brien Hill grove. The people of the boom town of Havilah, with its estimated population of 3,000 in 1866, may have similarly cut down and used nearby Piute cypress.

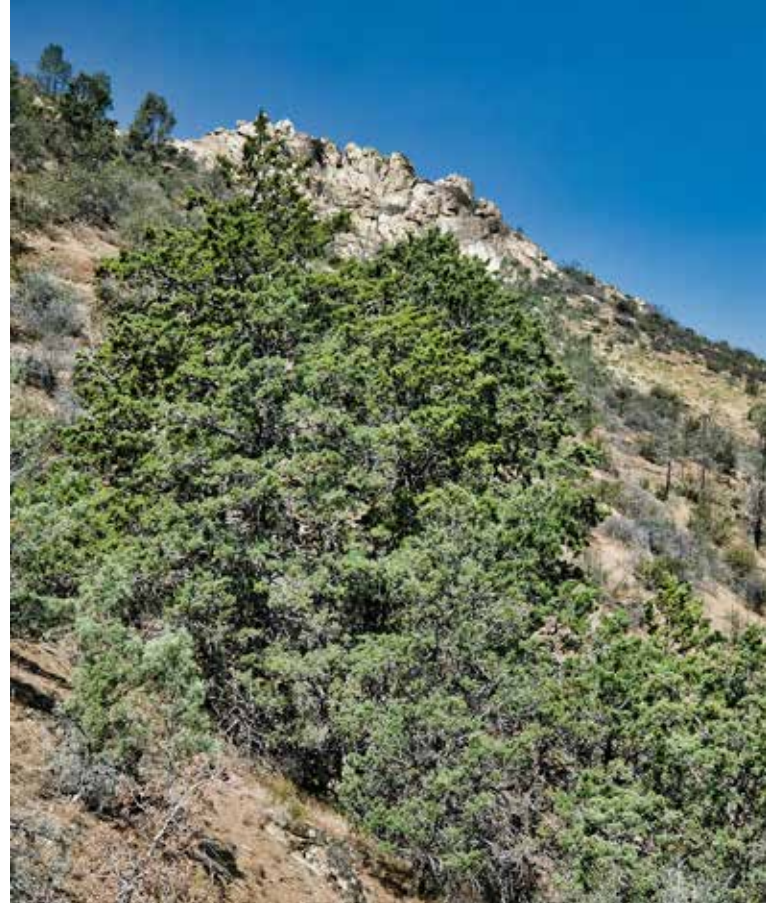
Piute cypress growing on the northern edge of the Long Canyon grove in 1981 prior to the Bodfish Fire in 1984. Kern Plateau, upper Kern River Valley, and Isabella Lake are visible in the distance.



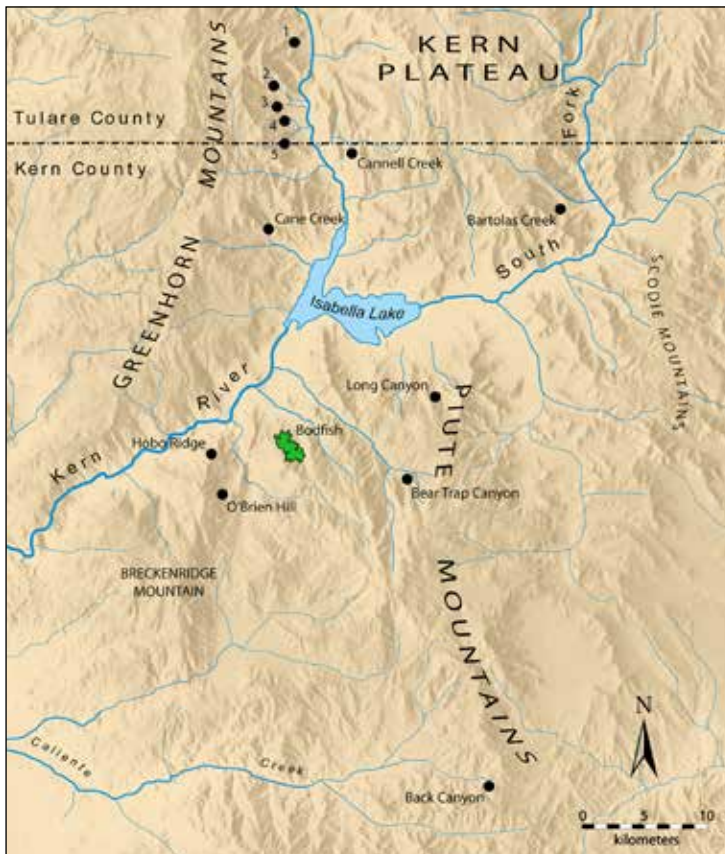
Well before the Kern County gold rush, one of the local indigenous American Indian tribes, the Kawaiisu that inhabited the Tehachapi Valley northward to the Piute Mountains, had several medicinal uses for Piute cypress. Such uses included a decoction of dried seeds to treat a sore chest and colds, and a hot or cold infusion of cones to treat menstruation and kidney problems. Though the tribal name “Paiute” is generally reserved for the Shoshone people of the Great Basin, the name Piute likely was applied to the Kawaiisu because of their Shoshonean lineage. This tribal identity likely was the etymological origin for the Piute Mountains. Because Carl B. Wolf of the Rancho Santa Ana Botanic Garden knew only of populations within these mountains, he gave Piute cypress its vernacular name in his 1948 monograph of the New World cypresses.

DISTRIBUTION, GEOLOGY, AND SOILS

Piute cypress is endemic to Kern and Tulare counties with most of its groves occurring in the Piute and Greenhorn Mountains. These small southern Sierran ranges flank opposing sides of the Kern River Valley. Excepting the



Piute cypress in the Cannell Creek grove in 2017.



Southern Sierra Nevada showing the range and location of the Piute cypress groves in Kern and Tulare Counties. Black dots represent the approximate location of Piute cypress groves that are too small to map grove boundaries at this scale. The green polygon depicts the Bodfish grove. The closely-grouped groves in the northern Greenhorn Mountains are: (1) Corral Creek, (2) Stormy Canyon, (3) “Unnamed” Canyon, (4) Dark Canyon, (5) Chico Canyon.

[Source: Updated from Bartel (1980).]

southernmost grove near the headwaters of Caliente Creek in Back Canyon, the species is restricted to the watershed of the Kern River and its tributaries. Reports from Fresno and Los Angeles counties are misidentifications of naturalized plantings of smooth Arizona and Tecate cypress.

Piute cypress grows at elevations between 3,600 and 5,900 feet, though occasionally a few scattered trees can be found below groves along watercourses. In an extreme example of cones and seeds traveling more than a mile downstream following a 1966 fire, several cypress saplings were found in 1977 on the fill slopes of a county road at 2,400 feet.

The dozen plus remaining Piute cypress groves are perched on isolated ridges and north- to east-facing slopes, on geological substrates that range from plutonic igneous rocks (including granite, granodiorite, and gabbro), to metasedimentary rocks (such as micaeous schist, quartzite, and limestone). While not entirely restricted to a particular substrate like Sargent cypress and serpentine, Piute cypress trees typically appear to be confined to clearly defined stands or groves that often seem to be delineated by edaphic or topographic features. For example, a couple of groves appear to be restricted to a particular rock type, while other stands seem to be confined to a particular aspect and elevation range.

The 500-acre Bodfish grove, by far the largest Piute cypress population, differs geologically from the other dozen groves. Specifically, the northwest portion of the grove grows on Bodfish gabbro, a complex mafic rock unit composed largely of olivine gabbro supplemented by several other serpentinized rock types. These dark rocks and the resulting clay soils from this portion of the Bodfish grove generally have higher quantities of iron and magnesium. These two elements give the soil its dark green—nearly black—appearance when wet and intense red color when dry.

The southeast portion of the Bodfish grove occurs on metasedimentary rock that consists largely of mica schist, interbedded quartzite, and crystalline limestone.

The abundance of light-colored limestone and quartzite in this part of the grove gives the loamy soil a light-brown hue compared to the darker tones of the northwest portion of the Bodfish grove. Similar metasedimentary rock underlies the Back Canyon grove with its skeletal loamy shallow soils derived from mica-ceous schist and quartzite. Likewise, most of the Cane Creek grove, including the backside of Black Mountain, is underlain by metasedimentary rocks consisting

mostly of schists; while metamorphic rocks, primarily metamorphosed quartzite, limestone, and shale, underlie the Long Canyon grove on the northern end of the Piute Mountains.

Granite and granodiorite underlie the remaining Piute cypress groves and grove portions. The fact that the majority of Piute cypress groves occur on granitic substrates is highly unusual for any western cypress species in California. While both natural populations of Monterey cypress grow on granodiorite on the coastal headlands near Cypress Point and on Point Lobos in Monterey County, half of the remaining eight California species have only a single population that occurs in whole or in part on a granitic substrate: Baker cypress near Independence Creek in Siskiyou County, Gowen cypress east of Point Lobos in Monterey County, Santa Cruz cypress near Majors

Creek in Santa Cruz County, and Tecate cypress on Tecate Peak in San Diego County. By population, these stands on granitic substrates represent less than 5% of the total non-Piute cypress occurrences in the state.

ASSOCIATED VEGETATION, LONGEVITY, REPRODUCTIVE BIOLOGY, AND FIRE HISTORY

Probably due to the soils and aspect within the northwest portion of the Bodfish grove, older Piute cypress dominates the associated woodland trees more than in any other grove. The trees in the older stand average 250 years in age or more, although a few scattered individuals are an estimated 400–650 years in age. While a few of the trees approach 40 feet in height, most are in the 20–30 foot range. The other tree species associated with Piute cypress, in descending frequency, are singleleaf pinyon pine (*Pinus monophylla*), California juniper (*Juniperus californica*), blue oak (*Quercus douglasii*), and gray pine (*Pinus sabiniana*). With few shrubs and little herbaceous vegetation, nothing but cypress and open rocky clay soil can be seen when you're walking through this older stand of the Bodfish grove. Though small pinyon saplings can be found scattered throughout the grove and blue oaks invade the lower periphery of the older stand, the slow and nearly suspended growth of this large older stand has made the Bodfish grove appear unchanged since its discovery.

In contrast, the younger stand in the southeast portion of the Bodfish grove has been subjected to multiple fires, the last two occurring in 1921 and 2010. As a result, chaparral shrubs grow in lieu of the woodland trees found in the older stand because such trees require many fire-free years for establishment. The shrubs, in descending frequency, are Mojave ceanothus (*Ceanothus vestitus*), whiteleaf manzanita (*Arctostaphylos viscida* subsp. *viscida*), flannelbush (*Fremontodendron californicum*), birch-leaf mountain-mahogany (*Cercocarpus betuloides*), shin oak (*Quercus garryana* var. *semota*), silk tassel bush (*Garrya flavescens*), chaparral yucca (*Hesperoyucca whipplei*), green ephedra (*Ephedra viridis*), and California yerba santa (*Eriodictyon californicum*). The similarly burned Long Canyon grove has the same associated chaparral shrubs.

Like the older stand of the Bodfish grove, the Back Canyon grove has not experienced fire for an extended period of time, an estimated 180 years. Though some of the cypress trees approach 30 feet in height, many are considerably shorter. The associated woodland species, in descending frequency, are Tucker's oak (*Quercus john-tuckeri*), singleleaf pinyon, California juniper, and blue oak. These native woodland species have continued to expand their numbers within the grove over the years and, together



Piute cypress tree growing in the southern portion of the older stand of Bodfish Grove in 2017.



Dr. Randall Terry from Lamar University in Beaumont, Texas, collecting genetic material in 2017 from the Back Canyon grove. Two conifers, singleleaf pinyon pine (*Pinus monophylla*) and California juniper (*Juniperus californica*), reproducing without the aid of fire, compete with Piute cypress in this grove that has not burned for an estimated 180 years.



Within the oldest portion of the Hobo Ridge grove, a small stand of Piute cypress averaging 50 feet in height in 1981 avoided fire for hundreds of years, including the fires of 1921 and 1966. Despite reports that the 2010 Canyon Fire again missed this stand, aerial imagery indicates that most of the tall trees did indeed burn.

with chaparral yucca and substantial herbaceous cover, have become increasingly dominant. This is in sharp contrast to the older stand of the Bodfish grove.

In the remaining groves that grow on granitic-derived substrate, Piute cypress struggle within a “sea” of chaparral that often stands over six feet tall. In light of the frequency of fire, chaparral shrubs dominate these generally small and isolated groves. On the northeast flank of Breckenridge Mountain, a few of the oldest trees in the Hobo Ridge grove have somehow escaped fire for more than an estimated 500 years and stand 50 feet tall despite fires sweeping through the grove as recently as 2010. While buckbrush (*Ceanothus cuneatus* var. *cuneatus*) has replaced Mohave ceanothus in these granitic groves, the associated species include all of the shrubs growing in the younger stand of the Bodfish grove as well as big sagebrush (*Artemisia tridentata* subsp. *tridentata*), California yerba santa, canyon live oak (*Quercus chrysolepis*), interior live oak (*Quercus wislizeni*), western poison oak (*Toxicodendron diversilobum*), and gray pine.

Maturing the second year, the woody seed cones of Piute cypress (and most species of western cypress) are serotinous and thus gener-

ally remain closed and attached for years beyond maturity. About a hundred seeds are packed tightly in the oblong to ball-shaped cones of the species. The annual production and accumulation of seed cones over time within the canopy of mature cypress creates a canopy seed bank within each stand or grove. Because cones do eventually open and drop their seeds, seedlings can be seen on occasion within patches of open and disturbed ground such as cut slopes and stream borders. This phenomenon occurs with all western cypress species to varying degrees.

Below left: Branch with mature seed cones from the Long Canyon grove in 1981. Below right: Newly germinated seedling in 1985 from the Long Canyon grove following the Bodfish Fire in 1984.



As evidenced by the oldest trees in the Bodfish and Hobo Ridge groves, Piute cypress can live for hundreds of years in the absence of fire. However, because individual trees rarely survive fire and cannot resprout after burning or scorching, the species depends upon an adequate canopy seed bank to ensure sufficient reproduction after the next inevitable fire. Since the species does not produce any seed cones until its saplings reach six to 13 years in age, Piute cypress could be vulnerable to fire return intervals that are too short, perhaps 20 to 30 years. While studies of closely related Sargent cypress showed that regeneration after fire was substantial in stands as young as 21 years (Ne'eman et al. 1999), the large population studied was comparable to the older stand of the Bodfish grove and not like the remaining small fragmented groves, especially those occurring on granite and granodiorite.

In an example of the effects of repetitive fire observed within a short timeframe, the four adjacent groves in the Greenhorn Mountains were difficult to view in 1978 from the Kern River, even with the aid of binoculars and morning light. As problematic as it was to see these Piute cypress groves at the time from the river and adjacent highway, it was even more difficult to visit them. Because the area had not burned since the locally infamous Bull Run fire in 1924, the trees were engulfed by dense chaparral and oaks up to 12 feet tall. Not surprising given the density of the vegetation,

the 1990 Stormy Complex fire burned intensely within the Stormy Canyon grove and portions of the two groves to the south. The fire was so powerful in places that no snags were left, just holes where trees once stood. The sudden intense heating of granite boulders by the fire resulted in an austere looking landscape, with spalled rocks lying on the deep white fluffy ash. Unfortunately, the 2010 Bull fire swept much of the same area 20 years later, affecting



Burned Piute cypress tree in Stormy Canyon grove following the Stormy Canyon Complex Fire in 1990.

all four groves this time, including the Chico Canyon grove further south. While infrared imagery and U.S. Forest Service fire maps confirm that portions of these four groves did not burn, the long-term effects of these repetitive fires on these small groves is not known.

Many people are familiar with the iconic-shaped Monterey cypress that adorns the rugged and picturesque headlands of its natural range along the Central California coast. Because this species is widely planted and its cones often open a few years after maturity, naturalized Monterey cypress can also be seen along much of the much-visited California and Oregon coasts. Some people are also familiar with the Mendocino (or Pygmy) cypress and its dwarfed individuals that grow on sterile hard-pan soils of former ancient beach terraces. By contrast, while many people don't know of Piute cypress, this species may represent the best example today of a relictual western cypress; that is, a formerly widespread species that grew without regard to substrate and, since the Pleistocene, has been reduced to widely distributed, isolated groves. We expect that ongoing genetic studies comparing many of the populations of Piute cypress with its five nearest relatives will confirm that these western cypresses are relictual and not a product of long distance dispersal. Regardless of the answer to this academic question, we now seem to be witnessing the shrinkage—if not yet the complete disappearance—of several Piute cypress groves in the face of the increasing repetitive fires that are likely a more prominent feature of climate-changed California.

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—Jim A. Bartel, jbartel@sdbgarden.org

CALIFORNIA'S CYPRESSES: PORTRAITS IN DIVERSITY & ISOLATION

Glenn Keator and David Loeb

One of the most photographed natural places along the California coast is the iconic wind-sculpted “lone cypress” along 17-Mile Drive in Pebble Beach. This famous Monterey cypress, like those pictured below, is one of ten western cypress (genus *Hesperocyparis*) species found in California. Their often twisted trunks, picturesque crowns, and rugged appearance, suggest strength and old age. But appearances can be misleading, for most cypresses are relatively short-lived, living less than 100 years.

The genus *Hesperocyparis*—to which all the western cypresses belong—is a relatively recent split from the Old World cypresses in the genus *Cupressus*. The diversity of western cypresses in our state is notable, as California is home to far more species than are found in any other state.

All western cypresses are monoecious, meaning that both pollen and seed cones are on the same plant. The pollen cones are produced by the thousands, releasing pollen late in the year before winter rains, while the seed cones take a full two years to ripen. Once mature, the seed cones can stay tightly closed for years, opening only when aged or exposed to extreme heat or fire. Even after the cones open, they can remain tightly attached to the tree.

An interesting feature of our western cypresses is their preference for soils low in nutrients—such as serpentine- or sandstone-based soils—where competing trees have a harder time growing. This feature is perhaps responsible for both their diversity and their relative isolation from each other, with most species found only within a small range.

Here we present a gallery of all the California *Hesperocyparis* species, except for the Piute (*H. nevadensis*), featured in greater depth in the article on page 23.

[Text adapted in part from “*Hesperocyparis, the Western Cypresses*” by Glenn Keator, *Manzanita*, Vol. 22, No. 3, Summer 2018 (published by the Friends of Regional Parks Botanic Garden, Berkeley, CA)]

MONTEREY CYPRESS

The only native stands of this most famous of the California cypresses, *Hesperocyparis macrocarpa*, are found along 17-Mile Drive in Carmel and a few miles to the south at Point Lobos State Park, straddling the rocky granitic promontories west of Highway 1. However, the tree has been widely planted in coastal regions of California (such as in Golden Gate Park) and around the world. Monterey cypress distinguishes itself by having an asymmetrical crown, the branches often horizontally trending (though wind causes some of the shaping), with deep green foliage and (mostly) larger seed cones. [Glenn Keator]





MACNAB CYPRESS

H. macnabiana is relatively easy to identify because it forms a dense tall shrub with multiple trunks sporting fibrous, furrowed bark. From a distance, it has a decidedly gray appearance. Unlike others in the genus, MacNab cypress has flattened branchlets lying all in one plane, forming a spray, instead of a bristle. It grows on serpentine barrens in the northern Sierra foothills (including on steep slopes above the town of Magalia in Butte County, burned in the November 2018 Camp Fire) and the inner coast ranges of Napa, Lake, and Glenn counties (including on Walker Ridge just west of the wildflower mecca, Bear Valley). [Glenn Keator]



BAKER'S CYPRESS

H. bakeri is scattered in mostly small groves above 3,000 feet in the Siskiyou Mountains of northern California and southern Oregon, north of Mt. Shasta. The tree, which grows up to 100 feet tall, is difficult to distinguish visually from the Piute cypress (*H. nevadensis*), and like the Piute, grows only on nutrient-poor substrates (serpentine soils or lava flows). Fortunately, their geographic ranges are far apart, so you would not confuse them in the field.

Joey Santore



Glenn Keator



Glenn Keator



CUYAMACA CYPRESS

H. stephensonii is a tree that grows to 30 feet or more, with gray-green foliage, a straight central trunk, and smooth, exfoliating cherry-red bark. Restricted to nutrient-poor soils within the King Creek watershed of Cuyamaca Rancho State Park in San Diego County, it is likely one of the rarest of the western cypresses. Most of this only-known population burned in the Cedar Fire in 2003; it is too early to tell if the population will regain its former numbers. [Joey Santore]



TECATE CYPRESS

H. forbesii is closely related to *H. stephensonii* and is likewise restricted to a small number of sites with nutrient-poor soils in the mountains of Southern California. You will find it in scattered groves of the Santa Ana Mountains (such as in the photo below, from near Anaheim) south to the border town of Tecate and into northwestern Baja California. It grows in shrub-like fashion to no more than 30 feet, and sports green foliage and smooth brownish to cherry-red exfoliating bark.



Glenn Keator

Joey Santore



SARGENT CYPRESS

H. sargentii is a relatively tall tree with dull gray-green foliage found only on serpentine substrates. It has the largest geographic range of the western cypresses, stretching from the inner north coast ranges, where it can overlap with *H. macnabiana* (the only case of overlapping ranges among California's cypresses), south to Cuesta Ridge in San Luis Obispo County. There is a large population on Carson Ridge near Mt. Tamalpais in Marin County, where the tree mostly assumes a dwarf form, due to the hot summer environment. [Steven Harper]



PYGMY CYPRESS

H. pygmaea got its name because it was first described from old marine terraces above the Mendocino coast that feature ancient sandy, heavily-leached, acidic white soils (called podzols) that support a pygmy forest consisting mostly of pygmy cypress and Bolander pines growing no more than 6-7 feet tall (as shown here at Jackson State Forest). However, it turns out that, despite its name, *H. pygmaea* is not a genetic dwarf, as trees of the species were later found in more fertile soils nearby that grow up to 150 feet, taller than any other of the western cypresses. [Teresa Sholars]





Jeff Reimer



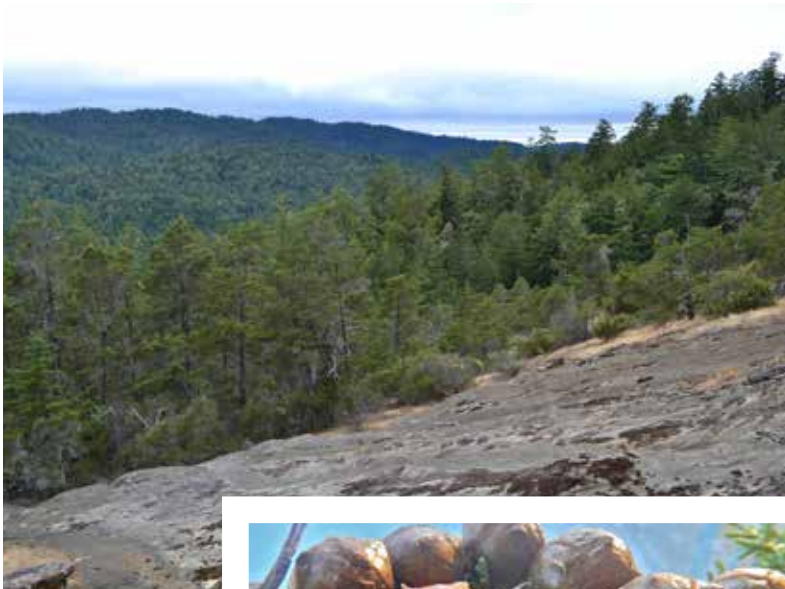
Steven Harper



Steven Harper

GOWEN CYPRESS

Arguably the rarest of the rare, *H. goveniana* is found only in two small areas near the Monterey Peninsula, where it comes close to, but doesn't quite meet, the Monterey cypress population. It grows on nutrient-poor sandy soils, like the closely-related *H. pygmaea*. Not a true dwarf, Gowen cypress remains a small tree (rarely more than 30 feet tall) featuring yellow-green foliage and a broad rounded crown. Its bark can be either smooth or rough.



Joey Santore



Joey Santore



Glenn Keator

SANTA CRUZ CYPRESS

H. abramsiana is also closely related to *H. goveniana*, but has dark green foliage and somewhat larger cones. It is only found in a handful of locales in the Santa Cruz Mountains (in Santa Cruz and San Mateo counties) at around 1,000–2,000 feet, on old sandstone-derived soils and ancient lithified sand dunes. It is shown here growing on Butano Ridge. It was listed by the U.S. Fish and Wildlife Service as an endangered species in 1987.



SUBALPINE SENTINELS: UNDERSTANDING & MANAGING WHITEBARK PINE IN CALIFORNIA

Michèle Slaton¹, Marc Meyer², Shana Gross³, Jonathan Nesmith⁴, Joan Dudney⁵,
Phillip van Mantgem⁶, Ramona Butz⁷

“The slender lash-like sprays of the Dwarf Pine stream out in wavering ripples, but the tallest and slenderest are far too unyielding to wave even in the heaviest gales.”

—John Muir refers to whitebark as Dwarf Pine in *The Mountains of California*, 1894

A WIDESPREAD SPECIES AT RISK

A hardy inhabitant of the subalpine zone of western North America, whitebark pine (*Pinus albicaulis*) is a keystone tree species in California’s subalpine forests, where it regularly defines the upper treeline in the Sierra Nevada, Cascade, Warner, and Klamath Mountains. Walking portions of the John Muir Trail in the southern Sierra Nevada, moving through extensive stands and mats of whitebark, one might wonder why such an apparently widespread and hardy species would be under consideration for listing as a federally endangered species.

Though whitebark is not uncommon in California, there is growing concern for its persistence, given recent observations of increased mortality, which may be exacerbated in coming decades due to the effects of climate change (Millar et al. 2012, Moore et al. 2017, Meyer and North *in press*). It is such concerns, in addition to dramatic and rapid declines throughout much of its range, that have led to proposals for listing this species under the federal Endangered Species Act (USFWS 2011). Indeed, as we go to press, status information related to listing is under review by the U.S. Fish and Wildlife Service (USFWS).

Figure 1. Whitebark pine cluster with basal sprouts on Table Mt., Bishop Creek, southern Sierra Nevada. [U.S. Forest Service]

In 2013, the U.S. Forest Service (USFS) placed whitebark pine on its Sensitive Species list in California. As a result, activities that could potentially affect the species must be evaluated under the National Environmental Policy Act. Nonetheless, there are relatively few studies that address the condition and health of whitebark pine in California, as distinct from elsewhere in western North America. Comprehensive management for whitebark pine was addressed in a recent range-wide restoration strategy (Keane et al. 2012), but this is largely focused on the Rocky Mountains and Pacific Northwest, due to relatively high impacts in these regions from threats such as mountain pine beetle outbreaks, white pine blister rust, climate change, and fire exclusion (Keane et al. 2012, Keane et al. 2017). So while these threats have caused precipitous declines of whitebark outside California, the southern Sierra population, for example, remains relatively healthy (Nesmith et al. 2019).

This means there is a high degree of interest among scientists, land managers, and stakeholders in gaining a better understanding of the potentially unique attributes of California's whitebark populations, which could serve a critical role in future management strategies. Even so, California is the only region that does not currently have an active genetic restoration program for whitebark. In other regions, these programs often include the collection, breeding, and planting of stock resistant to the non-native invasive pathogen, white pine blister rust. Current prospects for the development of such a restoration strategy and reforestation program in the state are promising, but these efforts will require considerable effort, cost, and coordination (Maloney et al. 2012). Here we review the most recent work evaluating whitebark health and status in California, and present the initial findings of a collaborative effort to establish a baseline of stand structure and health for continued monitoring.

A MAPPING CHALLENGE

At its highest elevations, whitebark often occurs in pure or nearly pure stands, resulting in geographically isolated stands on mountaintops. Most often found on windswept alpine and subalpine slopes and ridges, whitebark can either develop an upright stature or occur in krummholz (German for "twisted wood") cushions, or clumps, forming sometimes impenetrable islands that may exceed an acre in

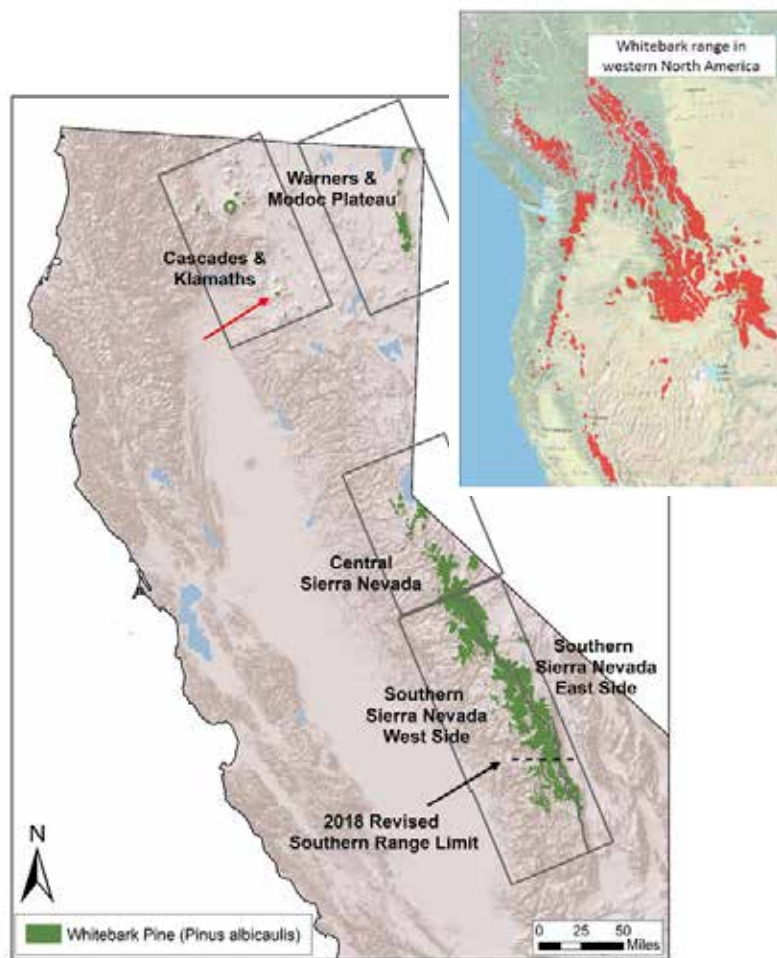


Figure 2. Distribution of whitebark in California, by geographic zone. Surveys revealed much more limited distribution at the southern range limit, with only two very small populations confirmed south of the revised boundary. Red arrow indicates highly isolated populations of Klamaths. Inset courtesy Whitebark Pine Foundation. [<http://whitebarkfound.org>]

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Figure 3. (a) Whitebark pine cones [D. Pechurina], and (b) a cluster of seedlings and now empty seeds, cached in the soil by animals [USFS].

size. Its success at high elevations can be attributed in part to tolerance of cold temperatures and adaptation to a short growing season, as well as to its structural ability to thrive near the ground surface, and thus remain protected from winter winds and desiccation under snow. Generally regarded as a disturbance-tolerant, early successional species, whitebark can be a first colonizer following a rockslide, avalanche, or stand-replacing fire. Yet on the harshest sites at or near treeline, it often forms “climax” communities where it is the dominant species (Arno and Weaver 1990).

Lower, stands are typically co-dominated by mountain hemlock, lodgepole pine, foxtail pine, western white pine, limber pine, and red or white fir (*Tsuga mertensiana*, *P. contorta* ssp. *murrayana*, *P. balfouriana*, *P. monticola*, *P. flexilis*, *Abies magnifica*, *A. concolor*, respectively).

Although whitebark has a broad geographic range, precise abundance and distribution information for California is limited. In 2014, the USFS compiled an updated map for whitebark-dominant stands, based on the CalVeg dataset (USDA Forest Service 2013a), 2012 National Insect and Disease Risk Maps (Krist et al. 2014), field visits, high resolution imagery, and aerial photography (Bokach 2014). Based on this effort, we estimated that there are 150,558 hectares (372,035 acres) of whitebark in stands greater than 0.4 hectares (one acre) in California.

Our more recent mapping and ground-truthing efforts in 2018 indicate that map improvements are still needed on over 20,000 acres, due to previous errors in interpretation of aerial photography and other imagery and also to the difficulty—even among experienced botanists—of determining species identity in situ if

cones are absent. The two main look-alikes are western white pine and limber pine (*P. monticola* and *P. flexilis*, respectively). You can distinguish western white pine in the field with a hand lens by noting the fine serrations on its needle-like leaves. But limber and whitebark pine are virtually indistinguishable, especially when young, before whitebark acquires its namesake color and develops mature cones. Given that the distribution of whitebark pine in California represents the southernmost extent of the species (Arno and Hoff 1989), and risk for populations occurring at their range edge is elevated (Slaton 2015), continued study and mapping of these populations is needed to identify their potentially unique genetic make-up and take potential action, such as seed collection or restoration, to ensure their continued persistence (Syring et al. 2016).

DEMOGRAPHY OF A SUBALPINE TREE

The seeds of whitebark pines are wingless and rarely dispersed by wind. Instead they rely on dispersion by squirrels or birds, primarily Clark’s nutcrackers (*Nucifraga columbiana*) (Arno and Hoff 1989, Tomback et al. 2001). These animals bury the seeds in the soil in small caches; if not reclaimed, the seeds may germinate and grow. Whitebark regeneration is therefore found most often in clumps, a form which can be accentuated by the tendency of lower branches to become pressed horizontally against moist ground from snow and then grow upright. Stems that do reach tree size (greater than 7.5 centimeters in diameter at breast height) are generally small compared to most other conifers, with height and diameter averaging 7 meters (23 feet) and 20 centimeters, respectively, in California (USFS, unpublished data).

Understanding the variability in stand structure and reproductive patterns between geographic regions can help to inform potential restoration strategies. For example, the relatively low tree density in the Warner Mountains, coupled with high proportions of conifers other than whitebark (namely, white fir) indicates that the sun-loving whitebark trees may be more vulnerable to being outcompeted by shade-tolerant species than in other regions of California. Also, whitebark's low reproductive success—sexual or asexual—in the Warner Mountains contrasts with the relatively high densities of young seedlings on the eastern side of the southern Sierra Nevada, perhaps indicating that success of planting efforts may vary by biogeographic region.

Finally, whereas previous studies have found increases in whitebark following disturbance in the southern Sierra Nevada (Meyer et al. 2016), we did not see this same correlation expressed at the scale of geographic regions—e.g. high recruitment rates in the Cascade and Klamath regions are coupled with relatively low disturbance rates. Such variable relationships emphasize how critical scale and ecological context are to understanding stand dynamics and planning restoration activities.

Given whitebark pine's broad geographic extent, consideration of genetic variation across regions is of utmost importance in developing potential conservation actions (Coutts et al. 2016). Studies are currently underway to assess regional genetic diversity and possible associations with climatic variables in central and southern Sierra Nevada whitebark pine populations (Elizabeth Milano, *personal communication*). In addition, we are finding whitebark stands at the edge of the tree's range in the southern Sierra Nevada undergoing proportional increases in recruitment of *other* conifer species, especially in the absence of disturbances that would create canopy openings and favor sun-loving whitebark (Slaton et al. *in review*). We did not observe this, however, in the interior part of its range. Thus, a revised southern distribution map may provide critical information on these vulnerable population segments.

A RESILIENT, YET VULNERABLE TREE

The USFWS designated whitebark pine as a candidate for listing under the Endangered Species Act in 2011 due to a suite of factors, including altered fire regimes; the introduced pathogen, white pine

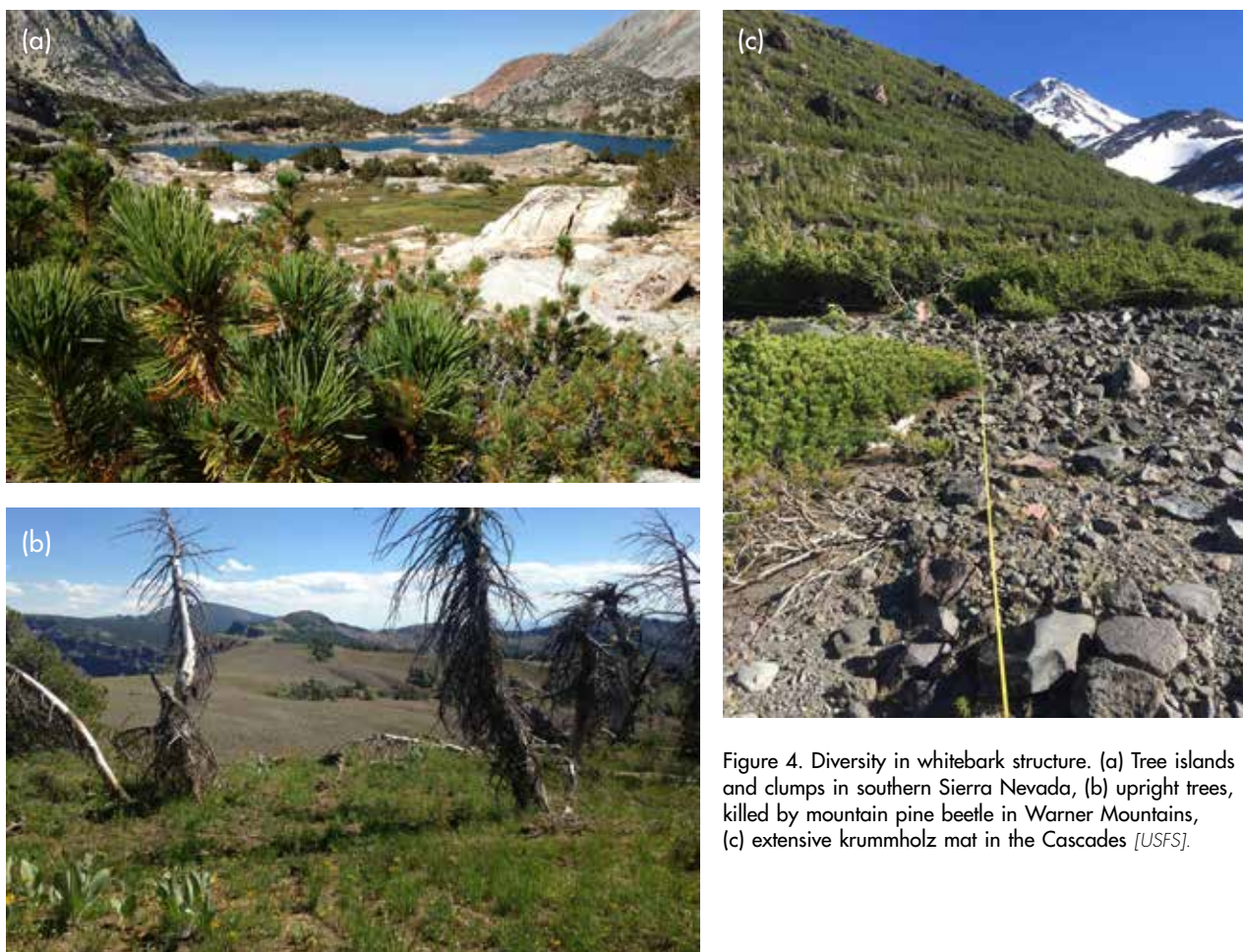


Figure 4. Diversity in whitebark structure. (a) Tree islands and clumps in southern Sierra Nevada, (b) upright trees, killed by mountain pine beetle in Warner Mountains, (c) extensive krummholz mat in the Cascades [USFS].

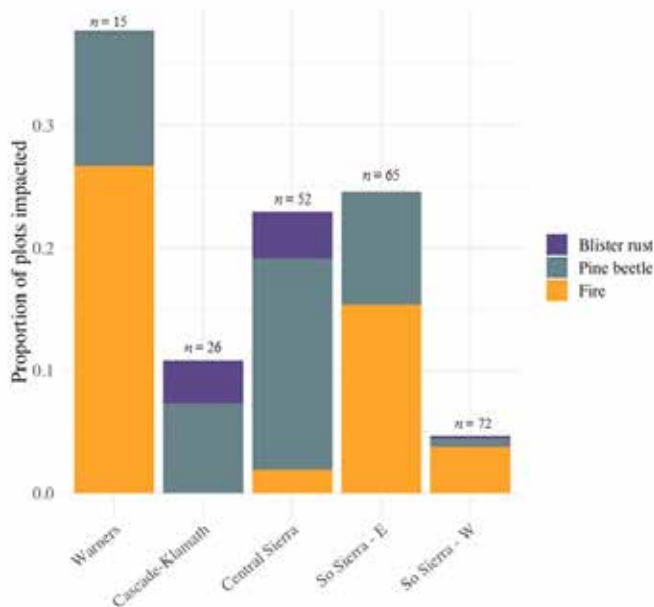


Figure 5. Geographic diversity in impacts of disturbance agents in whitebark ecosystems. Plot sample size indicated by n; data collected 2014-2018. Data combined from USFS and National Park Service protocols, plot size 0.12 - 0.62 acre (0.05 - 0.25 hectare). Other data sources indicate higher incidence of blister rust in central Sierra (Maloney et al., 2012); note USFS reports incidence by stem, whereas NPS reports by clump.

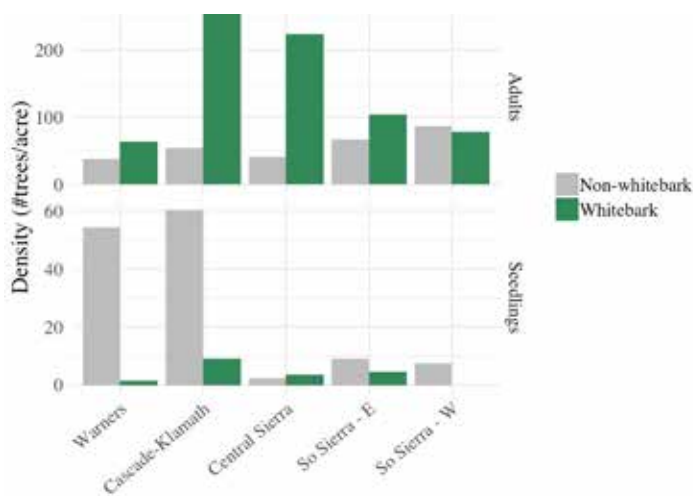


Figure 6. Variability in tree (> 7.5 centimeter diameter at breast height) and seedling (< 5 years old) density by geographic zone. Asexual regeneration is not accounted for here, although plots sampled in 2018 indicate highest basal sprout density in southern Sierra Nevada, and lowest in Warner Mountains. Sample sizes as in Figure 5; statistical analyses to be conducted following 2019 field campaign.

blister rust (*Cronartium ribicola*); mountain pine beetle (*Dendroctonus ponderosae*); and climate change (Tomback and Achuff 2010, USFWS 2011). These stressors have led to dramatic declines in whitebark across much of its range in the Rocky Mountains (Keane et al. 2012, Keane et al. 2017). Here we focus on how these threats are likely to affect whitebark populations in California in the future.

Changing fire regimes

Fire plays an important role in maintaining the health and resilience of whitebark pine forests throughout its geographic range. Historically, fires burned every 70 to 90 or more years in many upright (non-krummholz) stands, although researchers have documented shorter fire return intervals in other high-elevation forests (Murray and Siderius 2018, Meyer and North *in press*). Fire effects are variable, with some stands burning primarily at low severity (i.e., non-lethal surface fires) because of sparse surface and canopy fuels, and other stands burning at mixed severity (i.e., fire effects are highly variable over space and time) where trees are denser and fuels are spatially contiguous (Keane et al. 2012). Many areas in California are experiencing rapid shifts in fire severity, frequency, and extent, due to factors including warming temperatures, past fire suppression, and increased human ignitions (Keeley and Syphard 2016). We need more research and analysis to understand the current and projected changes in subalpine fire regimes in California.

Blister rust

Blister rust is an invasive pathogen native to northeastern Asia. It arrived in the United States around 1910 and spread through most of the range of whitebark pine and related five-needle (or white) pines, reaching the Sierra Nevada in 1968 (Kliejunas and Adams 2003). Whitebark is considered one of the most susceptible species of all the white pine hosts, including western white pine and limber pine (Kinloch and Dupper 2002).

Within the Sierra Nevada, blister rust occurrence and severity generally decline from north to south. For example, in Lassen National Park, Jules et al. (2017) found an average infection rate of 54% on whitebark pine. Maloney et al. (2012) found that, on average, 35% of individual whitebark pine trees showed symptoms of infection in the Tahoe basin, while Nesmith et al. (2019) and Dudney et al. (unpublished data) estimate that less than 1% of individual trees in the southern Sierra Nevada are infected. This trend is likely due to a combination of factors, including the relatively recent arrival of blister rust in the south, and the Sierra's relatively hot and dry climate. Although infections are still relatively low in the southern Sierra Nevada, Nesmith (2018a and 2018b) documents new observations of blister rust in Yosemite, Sequoia, and Kings Canyon National Parks.

Mountain pine beetle

The mountain pine beetle is native to western North America, including California, and is considered an important agent of disturbance in maintaining structural and compositional diversity of conifer forests (Weed et al. 2015). Recent warming trends have allowed the beetle to complete its seasonal life cycle at higher elevations, leading to increasingly common infestations in whitebark pine (Logan and Powell 2001, Mock et al. 2007, Kauffmann et al. 2014). It causes mortality by carving galleries through the xylem and phloem, and can be especially aggressive in drought-stressed trees. Although beetle outbreaks in California have been much lower compared to most other areas of its range, recent observations suggest this trend is changing and beetle populations are increasing (Millar et al. 2012, Meyer et al. 2016). Our data collection in 196 plots across the state from 2014 through 2018 indicated that mountain pine beetle is impacting 9% of whitebark pine trees. Many trees with symptoms of past attack have survived, and the chance of survival varies by region. For example, statewide, roughly one-half of attacked trees died; however, in the Warner Mountains, 100% of the attacked trees appear to have died.

Climate change

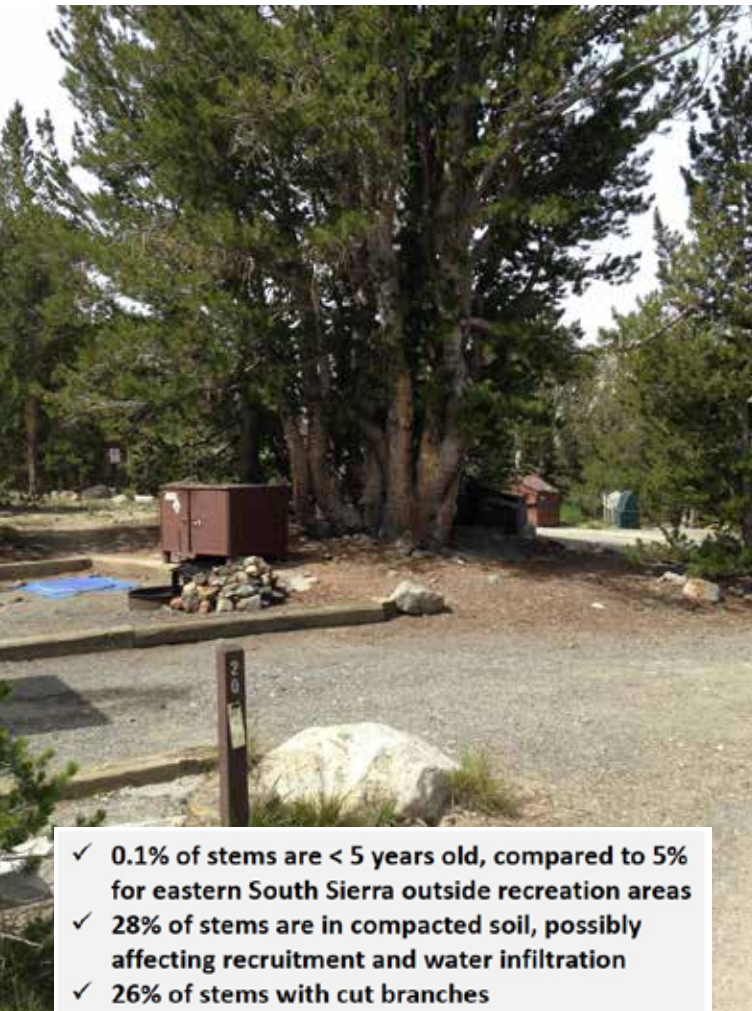
Studies are currently underway to understand the impacts of warming temperatures, drought, and climatic water deficits on whitebark growth and survival in the Sierra Nevada. Dolance et al. (2013) has presented evidence that warming temperatures may increase recruitment and promote survival of small trees, leading to shifting stand structure weighted toward smaller, younger trees. However, temperature-induced increases in aridity may exacerbate physiological stress and susceptibility to mountain pine beetles (Logan et al. 2010, Millar et al. 2012, Moore et al. 2017). In addition, low minimum temperatures are known to control both beetle and blister rust spread (Weed et al. 2013). Thus, rising temperatures may facilitate an upward expansion of both blister rust and beetles to higher elevations, creating concern for the long-term outlook of whitebark pine.



Figure 7. Threats to whitebark pine: (a) Severe mountain pine beetle attack at June Mt. Ski Area, southern Sierra Nevada [B. Oblinger]; (b) mountain pine beetle galleries [USFS]; (c) pitch produced by whitebark to expel mountain pine beetles [USFS]; (d) white pine blister rust aeciospores on whitebark. [USFS]

FOREST MANAGEMENT: SCIENCE IN ACTION

Active forest management of California's whitebark stands has been exceedingly limited for several reasons. First of all, the stands, which are mostly located in wilderness or roadless areas, are relatively inaccessible. And secondly, they are found in more "natural" conditions that appear relatively unaltered from historic reference conditions, and therefore don't *need* much active management for restoration (Meyer and North *in press*). Nonetheless, prescribed fire (wildland fire managed for resource objectives) has been identified as an important resource management tool elsewhere in the western U.S. for restoring whitebark pine forests that may have experienced decades of fire exclusion (Keane et al. 2012). In addition, USFS has recently implemented several forest management projects in whitebark stands within ski resorts in the Sierra Nevada. These projects provide an opportunity for us to better understand the effects of forest management treatments and mitigation measures on whitebark in California.



One example is the 2018 initiative by the USFS Lake Tahoe Basin Management Unit and Heavenly Mountain Resort to develop a proactive whitebark management plan. The intent of this Whitebark Pine Partnership Action Plan is to minimize impacts from threats and to foster restoration by undertaking the following actions: (1) restore stands and increase resilience to stressors through mechanical thinning and prescribed burning; (2) reduce white pine blister rust where feasible by pruning and/or removing infected trees; (3) promote stand regeneration through canopy gap creation; and (4) collect viable seeds for genetic testing and planting.

Another example is the emerging partnership of the Inyo National Forest, Mammoth Mountain Ski Area, National Fish and Wildlife Foundation, and CalTrout to restore whitebark pine stands impacted by mountain pine beetle and drought in the June Mountain ski area. The project is designed to increase stand resilience to future bark beetle attack and climate change; promote and protect natural whitebark pine regeneration; reduce hazardous fuels associated with amplified tree mortality (which decreases wildfire risk to the nearby community of June Lake); and improve watershed function. In both examples, engaged partners will monitor the effectiveness of the treatments and evaluate long-term trends in ecosystem health.

Additional opportunities for restoration may exist in whitebark stands found in several accessible spectacular areas—with dramatic peaks and gorgeous subalpine lakes—that attract large numbers of recreational visitors. Potential impacts from recreational activities, such as trail system use and camping, are not well understood. So the Inyo National Forest recently undertook an assessment of impacts to whitebark pines in four major watersheds in the eastern Sierra Nevada where paved roads, campgrounds, and trailheads occur in whitebark habitat. Recruitment in these areas is extremely limited, and mature trees are affected by soil compaction and by branch and stem cutting. While these impacts occur in only a small portion of the whitebark's range, site accessibility and public visibility make these areas excellent candidates for potential restoration and educational activities related to whitebark pine health.

Figure 8. Results of a recreational impact study conducted by the Inyo National Forest for six popular recreation areas with campgrounds, trailheads, parking lots, and/or boat launches in whitebark habitat. Photo taken at Saddlebag Campground, Tioga Pass area. [USFS]

MONITORING

Recognition of the variability in whitebark pine among geographic regions has inspired our recent monitoring efforts in California, which we hope will provide guidance for appropriate restoration strategies. For example, we are studying the benefits of re-introducing fire in areas where it has apparently been long excluded (e.g. Cascades and Klamaths), whereas in the Sierra Nevada, we are identifying trees with genetic resistance to white pine blister rust to promote resilience in those populations.

As indicated above, there are relatively few long-term monitoring datasets for whitebark populations in California, due in part to the tree's low timber values and limited accessibility to its remote habitat and steep terrain. In addition, until recently, people have believed that conditions for the whitebark were stable. Just in the last decade, Millar et al. (2012) presented long-term trends based on tree-ring chronologies and USFS aerial detection surveys in which mappers estimated the extent and type of disturbance, finding localized, severe stand mortality in some portions of the southeastern Sierra Nevada and Warner Mountains. One of the very few examples of stand-level repeated measurements of whitebark pine is from a long-term U.S. Geological Survey study of a large (2.5 hectares) forest plot in Yosemite National Park, in which all trees have been censused annually since 1996. At this site, annual counts show that the newly dead trees generally outnumber newly established trees, suggesting a closer study of this site is needed (Das et al. 2013). This demographic trend has been occurring despite only recent and minor observations of white pine blister rust (Adrian Das, *personal communication*).

The National Park Service (NPS) Inventory & Monitoring program is another recent source for long-term monitoring data of whitebark pine. It began as a regional monitoring effort of high elevation white pines across several Pacific West Region parks in 2011. In Lassen, Yosemite, Sequoia, and Kings Canyon national parks, the researchers have established 94 of a planned 102 permanent plots (0.25 hectare) where trees are being individually tracked and assessed every three years (McKinney et al. 2012).

Implementing effective restoration requires an understanding of the ecological context of the target species (Keane et al. 2012). A broad-scale assessment of whitebark condition in California was initiated in 2014 by the USFS, complementing the existing network established on NPS lands. Such a monitoring network that adequately represents all geographic

regions—regardless of land ownership—provides the ability to inventory and monitor patterns of mortality and regeneration, and to determine the rate and causes of mortality. In addition, such a network can contribute to the development of restoration and adaptive strategies and help identify where to prioritize management actions. The USFS campaign was substantially expanded in 2018 to 166 plots (0.08 hectare), and will be completed in 2019, after which it will serve as a baseline for future studies. Among the pressing questions under investigation are:

- 1) Are there areas where regeneration is not keeping up with mortality?
- 2) Where are stressors having the greatest impact, and are the impacts expanding?
- 3) Are other high elevation conifers outcompeting whitebark pine, and what role do disturbance regimes play in that interaction?
- 4) Are there additional range distribution surprises, similar to the revisions we found in the southern Sierra Nevada? Isolated populations in the northern Sierra Nevada and southern Great Basin in California are ripe for exploration.

CONCLUSIONS

Until recently, stressors such as blister rust and mountain pine beetle have had relatively small impacts in California, compared to their impacts in other parts of western North America, where they have largely decimated whitebark pine populations. However, the continued spread and intensification of these stressors and their interactions with a rapidly changing climate may portend future whitebark declines in this region. Clearly, the diversity of California's whitebark stands, with their many different ecological settings, and potentially unique genetic composition, points to the need for a strategy for monitoring, conservation, and restoration that is tailored to each unique zone.

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LIMBER PINE'S WILD RIDE WITH CLIMATE: UP, DOWN, AND ALL AROUND

Text and Photos by Constance I. Millar

Despite its widespread distribution, broad ecological influence, and respectable longevity, limber pine (*Pinus flexilis*) remains little known next to its more charismatic cousins, whitebark pine (*P. albicaulis*) and Great Basin bristlecone pine (*P. longaeva*). A mountain species by nature, limber pine inhabits the subalpine zone across much of temperate western North America. In California, limber pine occurs sporadically in the mountains of southern California, the southwest Sierra Nevada, and the Great Basin (GB) portions of California east of the Sierra Nevada crest. Its range continues to the east, across the high mountains of the GB, where it extends from the woodland conifer community through the uplands to form the upper treeline. Limber pine's wide distribution in the GB, often as the only high-elevation conifer, means that it has critical ecological significance, sheltering and supporting the subalpine biome.

Limber pines can grow to 2,000 years old, and their dead wood can persist on the ground for millennia. These factors allow scientists to use limber pine to unravel climate and ecology of the past. Our recent and ongoing studies of limber pine's response to past and present climate change offer some insights that challenge generally accepted assumptions, and may be helpful for the future management and conservation of resilient subalpine forests in California and beyond.

Above: Limber pine is reproducing not only at and above upper treeline but also at middle elevations, as in basins near Crooked Creek in the White Mountains of California.

Beyond its role as a keystone species and indicator of climate history, limber pine—with its warm, wine-red bark and gnarled, twisted forms cast against stark, open landscapes—provides a worthy aesthetic equal to the better-known bristlecone pine.

Taxonomically, limber pine is a five-needled “soft pine” (Subgenus *Strobus*). At first appearance it is easy to confuse limber with whitebark and western white pines. The only reliable field characteristic for distinguishing it from its subalpine congeners—whitebark, western white, and bristlecone pines—is the seed cone, which has an intact structure with stout scales and large seeds that have a highly reduced wing. The bark is often plate-like in old-growth trees, and the crown often spreads at the top, and can take striking wind-blown and asymmetric forms. The seeds are distributed by birds, primarily Clark's nutcrackers (*Nucifraga columbiana*), while those of the related species that share its distribution—whitebark pine excepting—are wind dispersed.



The seed cones are the only morphological characteristic that allows limber pine to be distinguished from related pines. Note the stout, elongated cone when closed (longer and thinner than whitebark pine, sturdier than western white pine), the thick bracts on the open cone (thicker than western white pine), and the persistence of the cone on the stem when mature (whitebark pine cones are torn apart by Clark's nutcrackers on the stem).

ECOLOGY AND CLIMATE

In our region (California and the Great Basin), old-growth stands of limber pine are generally sparse, with little understory growth. In the mountains of Southern California, limber pine has a minor role in mixed conifer forests. The species becomes more prominent in the southern Sierra Nevada, where it occurs with whitebark pine, lodgepole pine (*P. contorta*), and/or foxtail pine (*P. balfouriana*). In the White Mountains, limber pine mingles with bristlecone pine. The species can also be found in several smaller mountain ranges east of the Sierra Nevada in California, including the Glass Mountains, Bodie Mountains, and Sweetwater Mountains. Limber pine grows throughout the sub-alpine zone to the upper forest treeline, although where it occurs with bristlecone pine the latter extends to higher elevations. In the interior GB, limber pine occurs across the “cool” mountain zones, often as the sole upland conifer above pinyon (*P. monophylla*)/juniper (*Juniperus osteosperma*) woodlands.



The distribution of limber pine in the Great Basin (within the white lines; large map), and range-wide distribution (inset).

As might be inferred from this sketch, limber pine tolerates dry and warm interior mountain climates, with summer rain being an important element. Long Mediterranean summers without moisture relief push limber pine to competitive disadvantage. Similarly, where winters are long with deep snowpacks, limber pine yields to whitebark pine in the Sierra Nevada, Englemann spruce (*Picea engelmannii*) in eastern Nevada, or firs (*Abies* spp.) in the northern GB ranges. Within the GB, bristlecone pine has the most similar climatic requirements to limber pine. Given that bristlecone pine generally out-competes limber pine on carbonate and quartzite substrates, in the mountain ranges where those soils are extensive bristlecone pine dominates. Whereas the opposite is true for the ranges dominated by non-carbonate substrates such as granite, which favor limber pine.

Left: Old-growth limber pine with strip-bark stem and spiral grain growing on barren volcanic soils on Glass Mountain, Mono County in California.

LIMBER PINE AS A CLIMATE-STUDY SPECIES

Much of what is known of limber pine's ecology and genetics comes from studies in the Rocky Mountain part of its range. More than a decade ago, to expand our understanding of the species across its range, my research team at the Pacific Southwest Research Station of the U.S. Forest Service chose limber pine in the GB as a focal species to study for its responses to climate change, including both natural historic variability and ongoing human-mediated effects. Why choose limber pine? Not only is it important to understand limber pine's ecology in itself, given its role in subalpine forests, but we contend that limber pine in the GB ranges is a useful proxy (indicator) for potential future conditions of the subalpine forests of the Sierra Nevada. The many mountain ranges in the GB—653 overall (Charlet 1996), including 37 that have peaks reaching above 10,000 feet (Grayson 2011)—provide useful redundancy for testing hypotheses. Further, these mountains experience a wide range of climates similar to, but usefully different from, the Sierra Nevada, thus providing a diversity of potential “climate futures” to study in a space-for-time context. In addition, fuel in the subalpine zone of the semi-arid ranges of the GB is sparse and landscape fires infrequent. With lack of fire and cool-dry conditions, limber pine dead wood can be preserved on site for many millennia, providing useful information about past conditions.

We use a variety of methods to study limber pine's historic responses to climate variability as well as the effects of current climate change. Primary among these is tree-ring analysis, which involves extracting a thin cross-sectional core of wood with an increment borer; this reveals the rings of the tree—alive or dead—extending from the pith (center of the stem) to the outer bark. From these cores we can determine the age of live trees and, using cross-dating methods, work back in time to estimate the age of dead wood. Such dating is approximate, because the pith can be missing due to heart-rot, and erosion can remove outer rings near the bark.

In addition to determining tree ages, at each location we evaluate the relative growth of all annual rings in every tree sampled (secondary cambial growth in trees) and develop what are called “standard tree-ring chronologies” for each population. From these, we assess the climate variables, derived from instrumental weather stations in the region of the limber pine sites, extending back to the late 1800s, that best correlate with limber pine ring growth. Limber pine growth

is complexly correlated to instrumental climate data, with smallest rings occurring when growing season temperatures are either very high or very low with low precipitation, and largest when growing season temperatures are warm and precipitation is high.

For understanding range shifts at local to regional scales in response to climate, we add demographic methods to tree-ring approaches, which enable us to know birth and death dates. With these combined approaches, we can estimate density of tree stems and cohort ages for current conditions and also tree densities in the past. We correlate data with climate information, once again, from instrumental weather stations, to infer modern responses of limber pine recruitment and death. For historic conditions we are lucky that many studies have reconstructed pre-historic climates in the GB, using inferences from proxies as diverse as glacial moraines, lake sediment cores, paleo-historic pollen and macro-fossil distributions, packrat middens, and tree-ring estimations. These provide climate analogs for past centuries and millennia that replace the direct observational values from instrumental records, which extend at best only 140 years into the past. Interestingly, correlations of limber pine recruitment suggest that the best annual conditions for stem growth also favor germination and seedling establishment.

MOUNTAIN CLIMATES AND SPECIES RESPONSE—NOT ALWAYS AS EXPECTED

“Mountain species will shift up in elevation as temperatures warm.” Some version of this statement is so widely accepted that it has become a truism about climate-change effects. Tied to this is the projection that as mountain species shift upwards in pace with changing temperatures they eventually “run out of space at the top of mountains and become extirpated.” An early and prominent example of this projection comes from the study of Hayhoe et al. (2004), who modeled California climate at 2020 under diverse emission scenarios, and projected 75–90% loss of alpine and subalpine forest vegetation in California as a result of “elevational squeeze.”

The basis for these assumptions and modeling projections derives from the phenomenon commonly experienced by mountain visitors that temperatures cool as one moves to higher elevations. Under specified standard conditions, this physical process is described as the “atmospheric lapse rate,” in which, depending on location, the temperature declines between 6.5°C and



Our colleague, John King, coring an old-growth limber pine on Mount Grant in the Wassuk Range in Nevada.

10°C with each one kilometer increase in elevation. At long prehistoric time scales (millennia), movements of many mountain conifers have been documented to follow expected climate patterns (Huntley and Webb 1989). Similarly, as anthropogenic warming accelerates, many mountain tree species have been found to be shifting their ranges upward (e.g., Beckage et al. 2008; Lenoir et al. 2008).

At closer inspection, however, the enormous topographic diversity of mountain ranges, from the broad scale of valleys and peaks to the more localized scale of talus slopes and rock boulders, dictates that the atmospheric lapse rate is commonly broken. Topo- and micro-climatic processes, such as cold-air drainage (creating inversions), wind funneling, variability in solar radiation, and many other processes, affect local air temperatures and influence biotic response. Further, the size and mobility of mountain species has much to do with how individuals react to climate: For instance, a tall tree engages with regional atmospheric conditions while a stunted krummholz pine (“pruned” and shaped by wind and cold) or an alpine cushion plant experiences a very different weather environment. Thus, mountain species should be expected to

respond to climates that they actually encounter rather than theoretical conditions based on standard processes such as lapse rates or generalized regional conditions.

RESPONSES OF LIMBER PINE TO PAST AND PRESENT CLIMATE

Given the potential for mountain species to respond in more ways than simply shifting uphill or going extinct, we set out to investigate the diverse avenues that limber pine has taken or might take to respond adaptively to climate change. And the species has given us some surprising results. Below I summarize a few of our relevant findings.

Movement Up With Warming (But With a Twist)

In GB mountain ranges, there are locations where limber pine seedlings are establishing above the current upper forest border, as the common assumption would predict for warming conditions. However, there are some unexpected elements associated with this pattern (Millar et al. 2015, Smithers et al. 2017). First, the locations where limber pine seedlings are recruiting above current treeline are extremely rare, especially given the abundance of environments and extensive high elevation slopes that appear suitable for such upward expansion. Second, there seems to be—with an exception—no obvious environmental or climatic pattern to where these locations for recruitment occur. The exception is, in mountains where both bristlecone pine and limber pine occur, that seedling recruitment above current treeline often (but not always) occurs where ancient dead bristlecone pine stems remain above the current treeline.

Another surprise: In these ranges, limber pine is leap-frogging above bristlecone pine; that is, limber pine seedlings are more abundant above the current treeline than bristlecone pines. Finally, whereas it might be expected that recruitment upslope would correlate with warming over the past century, in fact, it has been episodic, with a pulse of seedlings dated from 1963 to 2000. This late 20th century interval correlates with a period of warm-but-not-hot temperatures in the growing season, and abundant summer/autumn precipitation, apparently conducive to seedling establishment and growth. These conditions have been less frequent over the last 20 years as multi-year droughts coincided with ongoing warming that created unfavorable conditions for seedlings to establish.

What is the fate of leap-frogging limber pine relative to bristlecone pine? From our current vantage point, we cannot predict the long-term conditions above current

treeline. The limber pine surge might be transient; bristlecone pine might catch up; or it might leap over limber pine (bird distribution favors limber pine early in the race, but wind-dispersed bristlecone pine might dominate later); or something very different might occur. What we do know from observation is that both species are currently recruiting uphill in very limited alpine locations, and that healthy subalpine forests of both species span across more than 3,000 feet of elevation. At present, both species appear hale and hearty in the ranges where they have been common in the past, especially considering other demographic responses, as discussed in the following section.

Moving Out at Mid-Elevations and Down in Low-Elevation Ravines

Many studies that investigate the response of mountain species to climate change focus primarily on the upper elevation range of those species. In contrast, our studies also look at the dynamics of limber pine at other parts of its elevation range. This provides a different perspective to what is occurring “at the top.” In the same study where we evaluated seedlings above the current treeline, we also estimated ages and densities of limber pine at mid- and low-elevations (Millar et al. 2015). Interestingly, we found that the species is still reproducing at these locations, if at lower densities than above treeline, and during the same late 20th century time/climate period. At mid-elevations, we found that the locations where seedlings established beyond the forest edges occur most often in sagebrush steppe basins. We inferred that temperature inversions that occurred historically in these locations and restricted seedling establishment were being disrupted by warming, allowing recruitment into these shrub habitats. Once again, the ages of these seedlings coincided with the cohort above current treeline.

Perhaps most surprising to us was finding limber pine seedlings establishing *below* the current forest border. We found them most often in narrow ravines, often north-facing, and once again with similar ages to the other pulses of recruitment. This low-elevation phenomenon fascinated us, and we took it up in a subsequent study (Millar et al. 2018a), investigating lim-



Limber pine is reproducing not only at and above upper treeline but also at middle elevations, as in basins near Crooked Creek in the White Mountains of California.

ber pines at low elevations across 50 mountain ranges of the GB. We were surprised to find a significantly disproportionate abundance of limber pines distributed in low ravines. These were often extra-marginal to the main part of the species distribution, which occurred on high-elevation, open slopes far above the ravines. Unexpectedly, seedlings were thriving under deep, dark, and humid riparian canopies of willow (*Salix* spp.), cottonwood (*Populus* spp.) and water birch (*Betula occidentalis*); mature limber pines extend



Surprisingly, limber pine is also reproducing in the dense shade of lowland riparian vegetation, as here under water birch (*Betula occidentalis*) in the Toiyama Range in Nevada, where damp, organic soils usually exclude pine seedlings.

above the crowns of these gallery forests. From a network of datalogger observations and estimates from the PRISM climate model (Daly et al. 1994), we assessed that although, as expected, these locations were warmer than the uplands, humidities are higher under the riparian canopies, soil moisture is higher than along slopes, and wind desiccation less. From these and other investigations, we conjecture that low-elevation ravine sites have served prehistorically as climate refugia for limber pine in the GB and might be important locations for the species to persist in the warming future. As such, climate adaptation and conservation efforts would be wise to consider these unexpected locations for protection (Morelli et al. 2016).

Limber Pine Moves All Around, But Bet On North

The Wassuk Range of western Nevada looms over Walker Lake to its highpoint of 11,285 feet atop Mount Grant. In contrast to the blue waters shimmering below, the range's upper slopes are arid and mostly barren of trees. Above the pinyon-juniper zone, sparse stands of limber pine grow on northward aspects. Abundant dead stems of large limber pines are scattered on these slopes and, unexpectedly, on all other aspects, including across entire watersheds where there are now no living limber pines. Because the wood of these relict stems is well preserved in the dry climate and fire-free landscape, we were able to collect and date, using tree-ring methods, more than 500 stems from across the range's high slopes (Millar et al. 2018b). These dated continuously from the present back to 1983 BCE (before Common Era), thus yielding a record of more than 4,000 years. From these stems we evaluated two distinct types of responses to prehistoric multi-century climate periods, including the Late Holocene Dry Period, Medieval Climate Anomaly, Little Ice Age, and the contemporary warming century.

First we evaluated growth of annual rings across the millennia from limber pines on all slopes and found growth correlated to the same weather conditions as in our other studies of modern stands. Importantly, growth also correlated to the multi-century climate intervals in expected ways—that is, higher growth during warm-wet periods, and lower growth during hot-dry or cold-dry periods.

Such associations with climate periods was not the case, however, for our demographic evaluations. Because we had so many dated stems, we could fairly assess the presence, absence, and relative abundance of stems at different locations across 4,000 years. We found, first, that despite high climate variability, there was no evidence for elevation shifts up or down over time, despite the existence of abundant areas on the high plateaus where pines could have migrated. Second, although there were periods of colonization and extirpation on slopes of different aspects across the millennia, there was no significant correlation with the prehistoric climate periods. Importantly, only on the north slopes did pines persist continuously—without extirpation and in denser stands—across the 4,000 year record.

From these results we infer that non-climatic effects, such as seed dispersal by Clark's nutcrackers and the presence or absence of essential ectomycorrhizal fungi, likely play an important role in where and when limber pines can grow, trumping influences of climate. We conclude that north slopes, with their higher humidities, lower solar radiation, higher soil moisture, and denser shrubby vegetation, support limber pine growth and persistence across centuries, even during periods when the climate might otherwise appear less conducive for the species. Thus, north-facing slopes might also serve as long-time refugia for limber pine in GB mountains, and, along with low ravine sites, could be evaluated for protection in climate-adaptation and conservation efforts.

A FINAL UNEXPECTED OUTCOME: LIMBER PINE AND BARK BEETLES

Over the last two decades, bark beetle epidemics in pine forests throughout the West have startled biologists and the public alike for their magnitude and severity. In the Sierra Nevada, tree mortality



Left: Limber pine growing on north slopes above Walker Lake in the arid Wassuk Range, where stands of the species have found refugial conditions despite varied climates of the past 4,000 years.

in subalpine forests was not as severe as in mountain regions elsewhere in the western United States, and pockets of mountain pine beetle outbreak on limber pine and whitebark pine were relatively small. Limber pine was affected in the 1986-1992 drought (Millar et al. 2007), while whitebark pine was attacked in the 2007-2013 drought (Millar et al. 2012). We used tree-ring and demographic approaches to evaluate the effects of the beetle outbreaks on the two species. In both cases we were surprised to find that the beetles killed fewer than 70% of the large trees in affected stands. The silvical thinning that resulted actually provided better growth conditions for the trees, enabling them to survive subsequent pine beetle attacks. Trees that succumbed to beetle attack appeared to have been poorly adapted genetically to the warm-dry conditions of the 20th and 21st centuries but had been better adapted to the cold-wet conditions of the Little Ice Age (LIA) centuries (~1450-1900). The opposite occurred for trees that survived; they had grown poorly during the LIA but grew significantly better under the more recent warming climates. Finding the same result in both species, we concluded that the bark beetle mortality actually improved the silvical and genetic composition of the forests, providing them with greater adaptation to future warming. This finding, of course, would not pertain if no trees survived the outbreak.

CONCLUSIONS

Our studies with limber pine have provided insights into how subalpine native pines respond to climate change. These included not only expected shifts up in elevation with warming, but many surprising and unexpected responses as well. These findings remind us that in scientific research, as in conservation, we should look beyond the expected—biology often throws a curveball into our assumptions. From the findings about limber pine, we might anticipate designating and protecting refugia in such places as low-elevation ravines and north-aspect slopes. Further, while dying trees are not pretty to the human eye, and dead trees can (for a period of time) promote fire and other hazards, it is valuable to consider the role of native insects in promoting adaptation to future conditions in long-lived trees. These and other surprises, and their attendant conservation implications, will surely continue to arise as scientists probe more deeply into the actual—rather than assumed—responses of trees to climate change.

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COMING TO TERMS WITH THE NEW NORMAL: FOREST RESILIENCE & MORTALITY IN THE SIERRA NEVADA

Jodi Axelson^{1,2}, John Battles¹, Adrian Das³, Phillip van Mantgem⁴

The vast conifer forests of California's Sierra Nevada range inspire awe and create lasting memories. The size and longevity of these trees make them seem both otherworldly and everlasting. Indeed, their grandeur is such that visitors may not appreciate how these forests are connected to the larger landscape, and so there is little understanding that something as common as a drought could lead to the death of so many trees and trigger massive and irreversible changes in the nature of these forests (Box 1: Reflections on the California Drought). Although tree death is a natural and essential process, human activity is increasing the mortality rate to such an extent that it threatens the persistence of the "big tree" forests (Lindenmayer et al. 2012, Allen et al. 2015) we have come to associate with the Sierra Nevada. Here, we briefly explain how forests change, with a focus on the role of tree mortality. We then describe the large-scale tree mortality event that occurred in the Sierra Nevada resulting from drought and other disturbances, and the ongoing risks to Sierran forests.

FORESTS ARE DYNAMIC

When we experience a forest—whether a grove of massive giant sequoias (*Sequoiadendron giganteum*) or a windswept ridge of twisted bristlecone pines (*Pinus longaeva*)—it often feels timeless and eternal, long predating human presence. Trees are one of nature's most reliable timekeepers, preserving a record of the passing years for decades, centuries, or even millennia. Trees, and the forests they form, are highly dynamic, where the interplay of disturbance and recovery produces shifts in composition, structure, and function through time. It is through such disturbance that forests change, with the death of trees potentially putting the ecosystem on a new trajectory, whether at the individual stand or larger landscape scale.

Reflections on the California Drought

In high school, I joked to my friends that the drought was the best thing that could have happened to our weather. From 2012 to 2016, the peak years of my adolescence, it barely rained in Berkeley. Many of my friends—being responsible citizens—prayed for winter storms. But I secretly relished wearing sunglasses in February and sporting a glowing tan in March. After the four long years of drought, just as the joke began to feel tired, the previously cloudless skies swelled with moisture and turned dark for weeks at a time, soaking my sunny West Coast fantasy. My friends and I went back to our rain coats and galoshes as grasses greened up across the East Bay hills. I assumed the worst was over. It was not until a year later, while accompanying my dad, John Battles, on a trip to his research sites in the southern Sierra Nevada, that I realized how wrong I was. Along the winding roads where once lush mountainsides of regal trees had distracted us from the monotony of tires on asphalt lay a constellation of gray skeletons. It seemed that every other tree (though more like one in five according to my dad) had been struck down by some invisible plague. When we reached Yosemite National Park, the campsite I had stayed in as a child was almost unrecognizable. Brown trees, some still standing in their graves, others lying on the ground, dotted the campsite like a curbside after Christmas. Nearby in an open yard lay hundreds of tree trunks, cut with industrial precision and stacked in neat piles. I asked my dad if logging regulations had changed. He said no, humans had not been the cause of this tree mortality, at least not directly. While the grasses near our home had returned with the winter rains, for millions of trees across California, the drought spelled death. —Thomas Battles

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For forests, disturbances are defined as discrete events that change vegetation structure, resource availability, and the physical environment (White and Pickett 1985). Three key attributes of disturbances are:

- 1) Type: Fires, windstorms, landslides, and flooding are examples of abiotic disturbances; insect outbreaks, disease infections, and rodent damage are examples of biotic disturbance.
- 2) Spatial and temporal characteristics: At what scale is a disturbance occurring, for how long, and with what return period? For example, a root rot center may affect a relatively small area (< one acre) while a wildfire can affect hundreds to thousands of acres; a landslide may last ten minutes while a bark beetle outbreak can last for many years.
- 3) Disturbance interactions: Some disturbances may amplify another disturbance (synergistic effects) while others will dampen disturbances (antagonistic effects). Examples of synergistic effects include drought initiating bark beetle outbreaks, and root rot centers increasing the likelihood of blowdown. An example of antagonistic effects is the reduced drought stress experienced by trees exposed to ozone pollution (e.g., Cousins 2016).

Disturbances, whatever their origin, are often shaped through complex feedback loops. For example, climate strongly affects the frequency and severity of disturbances, which in turn mediates the impact on forest composition and structure. In addition to climate, forest structure and composition also greatly influence the type, frequency, and severity of disturbances.

FOREST RESILIENCE

Forests have long provided overlapping and not always complementary ecological, social, and economic benefits—thus there is no social consensus about what a “healthy” forest looks like. Therefore, rather than health, in this paper we will focus on “resilience,” which is the capacity of a system to absorb disturbances and remain in, or return to, a similar condition (Gunderson 2000). Resilient forests can be characterized as those whose underlying ecological processes continue to operate on any temporal or spatial scale in response to historical disturbance regimes with which they evolved. In forests that lack resilience, a disturbance can push them into a new state, permanently altering what had been there before. A Californian example might be a forest located at lower elevations or on a drought prone site that is adapted to low severity fire, but then burns at high severity, killing all of

the trees. It is possible that this forest will not naturally regenerate, but instead convert to a new state, such as chaparral, shrubland, or grassland.

In general, forests have been resilient to historical disturbance, but as they come under increasing pressure from novel stressors that they did not evolve with, there is no guarantee that they will remain so. Climate change; invasive insects, diseases, and plants; and changes to disturbance regimes all represent departures from historical conditions. A major unanswered question then, given the increasing scale of disturbance in the age of climate change, is if forests will be resilient to ongoing changes in the present and the future.

TYPES AND DRIVERS OF TREE MORTALITY

Trees provide enormous benefits both when they are alive and after they die. The importance of tree death is reflected in the variety of functions trees serve throughout their existence; and in death there is a continuum of ecological roles they serve due to their prominence within a given ecosystem (Franklin et al. 1987). Thus, tree death is a normal process that is continually occurring, usually at low rates for mature trees. However, background mortality rates can be far exceeded by episodic pulses of mortality and by large-scale forest diebacks. This spectrum of mortality rate, severity, and extent is driven by various mechanisms, such as: competition (e.g., for water, light, nutrients), disturbance (e.g., insects, diseases, fire, landslides), climate (e.g., drought, increasing temperature, decreased snowpack), and/or other stressors such as air pollution (e.g., ozone).

Background mortality can be defined as the average rate of tree death normally experienced in a forest in the absence of significant disturbance or environmental change. In old-growth temperate forests, background rates of mortality typically range from ~0.5–2% per year (Stephenson and van Mantgem 2005), but have increased rapidly in recent years, doubling in the last two decades in western North America (van Mantgem et al. 2009). Around the globe, vegetated landscapes have had to cope with human-related intensification of stressors, with climate change playing an increasingly important role. For example, many disturbances, such as drought, wildfire, and insect outbreaks, are either entirely or partially driven by climate (e.g., Park et al. 2013). The spatial extent and severity of these disturbances are highly dependent on both trends and extremes in air temperature and precipitation. As stressors intensify, historical disturbance regimes can change,



A large giant sequoia has fallen, creating a large gap in the canopy. The additional sunlight reaching the forest floor facilitates the regeneration of new trees. The downed sequoia continues to be an important part of the ecosystem as it continues to store carbon in the short term and, in the long term, slowly decomposes as myriad heterotrophic organisms colonize and break down the wood. [Nathan Stephenson, USGS]

TREE MORTALITY – TREE DEATH FUNNEL

The causes of tree death can be straightforward to identify or more difficult to recognize. A tree crushed by another tree, or struck by lightning, or burned in a fire can be assigned a cause of death with little difficulty.

Often, however, a tree's death is a result of complex interactions among multiple factors. For example, a tree might only be attacked by bark beetles after being weakened by a drought or damaged by a fire. Another tree, gradually weakened due to root disease or competition, might live for many years before finally succumbing to other, normally less potent or non-lethal factors. In other cases, a perfectly healthy tree might be killed by bark beetles because a drought has weakened enough nearby trees to cause major increases in beetle populations, leading to an outbreak. Manion (1981) developed the decline disease spiral, which is a useful concept to help generalize the process of tree mortality. However, this model suggests that disturbances are cumulative and sequential contributors to tree death. We suggest that a tree's risk of death can be better visualized as a "death funnel" that relates its vulnerability to disturbance agents to its overall health.

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Increases in tree mortality, or die-off events, were thought to be rare, and related to discrete disturbances. However, recent observations across multiple continents suggest that die-off events may be increasing, triggered by drought and/or high temperatures, possibly in response to global climate change (Allen 2010). In the future, continued warming and additional extreme events will likely occur with greater frequency and severity. Under such conditions "chronic disequilibrium" may result, where the system cannot recover to its prior state, ecosystem processes are altered, and time between disturbance events is insufficient for recovery (McDowell et al. 2018). Enter the era of "megadisturbances"—those capable of driving massive tree mortality that in extent and severity surpass anything recorded in recent human history, whose legacies persist for a very long time, and can compound other disturbances (Millar and Stephenson 2015). This is not simply academic: Forests provide vital services such as carbon sequestration, watershed health, and social-ecological benefits. Thus, there is a sense of urgency to understand the consequences of climate change on ecosystems and to identify and understand thresholds of forest decline and massive tree mortality before they occur.

In the tree death funnel, disturbances are not necessarily cumulative or sequential but rather, the farther the tree descends down the funnel, the more susceptible it becomes to a variety of mortality agents, some more potent than others [Figure 1]. In this framework, all the mortality agents remain present as potential threats that could lead to death of a tree. For example, a tree could have root rot that slowly reduces its health, so it moves down the death funnel; but when a drought stresses the tree further it is actually killed by an agent, such as wood borers, that is usually non-lethal.

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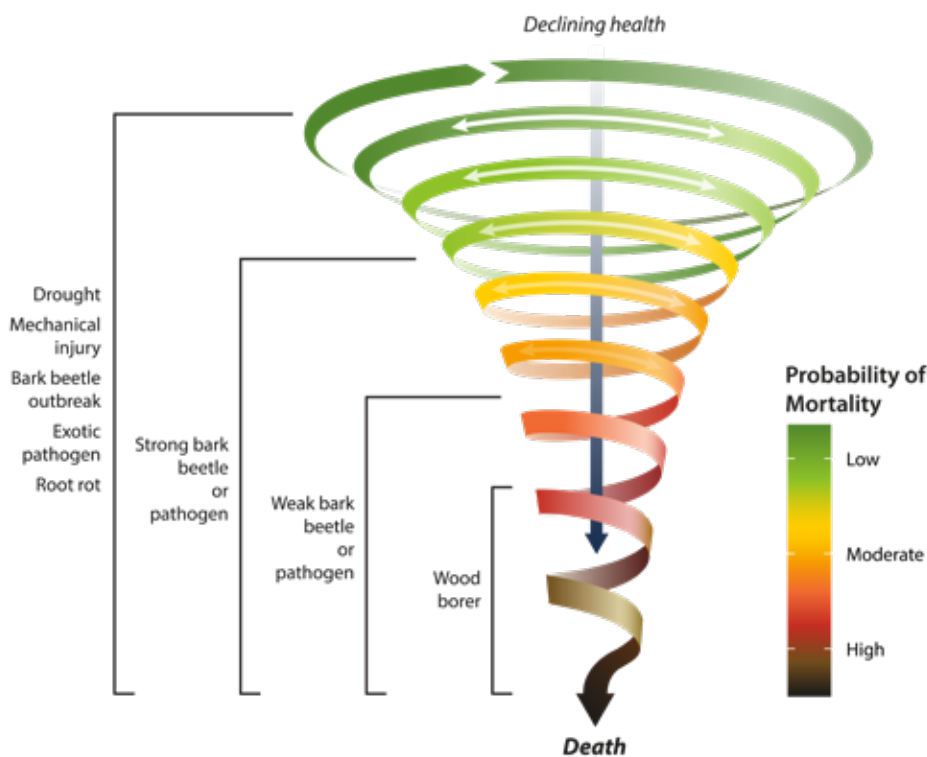


Figure 1. The conceptual tree death funnel shows that as the health of an individual declines, the risk of death increases, requiring less potent disturbances to lead to mortality. As conditions change, trees may recover and move back up the funnel (white arrows). However, the farther a tree declines down the funnel the less likely it is to recover (fading white arrows), until there is no escape and the tree dies.

when the drought ends the tree may recover, provided other disturbances, such as pathogens or bark beetles, do not kill it first. While many of the disturbances in the tree death funnel are biotic, many other abiotic disturbances, which are often stochastic in nature, can

kill a tree independent of its health status. For example a healthy and vigorous individual can be killed by events such as landslides, lightning strikes, or windstorms. The tree death spiral illustrates that death can be sudden (e.g., landslide) or gradual (e.g., root rot, drought, bark beetles), and that disturbances are not necessarily cumulative or sequential. Instead a variety of disturbances can potentially kill the tree and may have multiplicative effects.

Using the concept of the tree death funnel, a healthy sugar pine could be killed randomly by abiotic agents (e.g., lightning strike, windstorm, or high severity fire), or by biotic agents, or by interactions between these agents. If a sugar pine is infected with white pine blister rust it moves from a healthy state, down the death funnel, to a less healthy state. If a drought were to start, the sugar pine's health would likely continue to deteriorate, so now it would take less and less potent disturbance agents to kill it. If the sugar pine is far enough down the funnel, it may succumb to weak attack by mountain

pine beetles, which it cannot resist due to its poor health. At the extreme, even wood borers or twig beetles, normally considered minor threats, could be the proximate cause of its death [Figure 1].



Sugar Pine—a Fading Giant

Sugar pine (*Pinus lambertiana*) is a native conifer, dwelling in mid-to-high elevation mountain forests from the Cascade Range in north central Oregon to the Sierra San Pedro Martir in Baja California. The most extensive populations occupy the west slopes of the Sierra Nevada, where they range in elevation from 2,000 to 7,500 feet (Kinloch Jr. and Scheuner 1990). A mature sugar pine can be an unforgettable sight, given its massive height (175–200 feet), great gangly branches, and impressive long cones. In fact, sugar pines are second only to giant sequoias in terms of the sheer volume they attain in maturity. Sugar pine is a five-needle pine, along with whitebark (*P. albicaulis*) and bristlecone pines, and as such it is susceptible to the exotic fungal disease white pine blister rust (*Cronartium ribicola*). This invasive pathogen was first introduced to North America in the early 1900s and infects all five-needle pines, with sugar pine currently being the most susceptible species in California. In addition to the white pine blister rust, sugar pine is a host for the native mountain pine beetle (*Dendroctonus ponderosae*). In one study, researchers found that of all Sierran conifers, sugar pine has the highest incidence of biotic factors (66%) causing background mortality, with bark beetle attack (53%) and disease (30%) as the main drivers of mortality (Das et al. 2016).

Dead sugar pine with fading foliage in summer of 2018 above the shores of Lake Tahoe. Eventually red needles become gray and fall off, leaving behind a “ghost tree.” [Susie Kocher, UCANR]

MASSIVE TREE MORTALITY IN THE SOUTHERN SIERRA

Conifer forests are a defining feature of the Sierra Nevada range, being not only the most prevalent ecosystem but also the vegetation type that dominates ecosystem function (Dettinger et al. 2018). Disturbances such as fire, insects, and diseases have interacted to shape forests in California for millennia. Of these, arguably the dominant historical disturbance was fire, which was characterized by frequent (every 8-20 years) low- to moderate-intensity events in low- to mid-elevation forests. These historical fire regimes typically spared the large trees but killed smaller trees and other vegetation (Stephens et al. 2007). However, the nature of fire in the Sierra Nevada has been altered by fire suppression over the past century and more, and by the loss of the largest trees to timber harvests in the early 1900s. These cultural practices have created crowded forests with few larger trees, hordes of small trees, and uncharacteristically high levels of surface fuels (Butsic et al. 2017). These highly altered forests across the Sierran landscape are now facing the prospect of novel climates, which are significantly impacting disturbance regimes, with consequences for tree mortality.

Scientific studies suggest that drought stress plays a role in tree mortality patterns in California's Mediterranean climate (van Mantgem et al. 2009, Young et al. 2017). From 2012 to 2015, California experienced an epic drought whose hallmark was historic dryness and warmth (Swain 2015) resulting in record low levels of snow accumulation across the Sierra Nevada (Belmecheri et al. 2016). This extended aridity generated progressive canopy water stress in approximately 888 million trees across California (Asner et al. 2016) that ultimately induced a massive wave of tree mortality. In 2018, the U.S. Forest Service Forest Health Protection Program estimated that over 147 million trees on 9.7 million acres had died since 2010, with the greatest mortality occurring in the southern Sierra Nevada (USDA 2019). More specifically, from 2012 to 2017, the estimated loss of live trees was greater than 26% in the southern Sierra Nevada, compared to 2% in the northern portion of the range (Dettinger et al. 2018), representing an order of magnitude increase from north to south. Why was mortality so much greater in the southern Sierra Nevada? The primary driver was the higher drought stress experienced in this region (Young et al. 2017). Drought, likely exacerbated by crowded forests, resulted in amplified stress as trees



Dead and dying conifers pepper the landscape east of Moro Rock at the end of October 2015. An evergreen conifer tree is fully dead when all of its foliage is red, and in all likelihood dying when its foliage is yellow. For the pines pictured, it is unlikely that recovery is an option even for trees whose crowns are still yellow.

[Nathan Stephenson, USGS]

struggled to cope with high temperatures and record dry conditions. As the drought continued, and more and more trees became stressed across the landscape, they became increasingly susceptible to bark beetles, particularly mountain pine beetle and western pine beetle (*Dendroctonus brevicomis*), whose populations were rapidly increasing in response to an increasing number of vulnerable host trees. In Sequoia and Kings Canyon National Parks, lower elevation ponderosa pines (*Pinus ponderosa*) and sugar pines were the most susceptible (Paz-Kagan et al. 2017); by 2016, southern Sierra vistas were dominated by swaths of dying and dead trees.

This massive wave of abrupt tree mortality can be characterized as a megadisturbance and reveals the vulnerability of large portions of California's forest lands to novel conditions. Mortality, which occurred in all size classes, varied considerably by species [Figure 2]. Tree species that have bark beetle associates tended to have higher mortality levels than those species that do not. Many eruptive bark beetle species are native in the Sierra Nevada, such as fir engraver (*Scolytus ventralis*), which attacks white and red fir (*Abies concolor* and *A. magnifica*); mountain pine beetle, which attacks sugar pine; and western pine beetle, which attacks ponderosa pine. In a survey of hundreds of dead trees across 35 plots in Yosemite National Park, white fir and ponderosa and sugar pines experienced the greatest mortality,

while species such as incense cedar (*Calocedrus decurrens*) and black oak (*Quercus kelloggii*), which do not have eruptive bark beetle associates, experienced far less mortality [Figure 2].

The immediate effects of this widespread mortality have been, and will be, major reductions in live tree biomass, increased carbon emissions to the atmosphere as dead trees decompose, and major fuel buildup as dead trees fall down. Looking over the long term, there are more questions than answers. For example, will lower elevation ponderosa pines regenerate following severe mortality of this species in the southern Sierra Nevada (Fettig et al. 2019)? Or will other species, such as black oak and gray pine (*Pinus sabiniana*), come to dominate these areas? As shade tolerant species such as white fir and incense cedar become more dominant, how will ecosystem processes change? How does fire severity and extent change in response to heavy fuels? And do these changes result in firestorms, or “mass fires,” that burn over large areas and occur simultaneously (Stephens et al. 2018)?

THE FUTURE FOR SIERRAN FORESTS

The threats to forests in California will continue, and only increase, due to the impacts of climate change. Some of the most immediate threats in the Sierra Nevada will come from altered disturbance regimes, such as more frequent and hotter droughts leading to increases in insect outbreaks and mortality from compounding disturbances; severe wildfires that have abundant fuel to burn through; and type conversions at lower elevations at which the climate becomes too hot and dry to sustain forests as we know them now.

The major increases in forest mortality, particularly in the southern Sierra Nevada, are showing us that cherished forest landscapes may not be as resilient as we once believed. What might be done to respond to this challenge? What role can land managers play in mitigating unwanted impacts? Are there management practices used in the past that will continue to be useful in the future, or do we need to develop and implement a new suite of methodologies? Scientists are learning rapidly from these mortality events as they occur, hopefully putting us in a stronger position to make a difference.

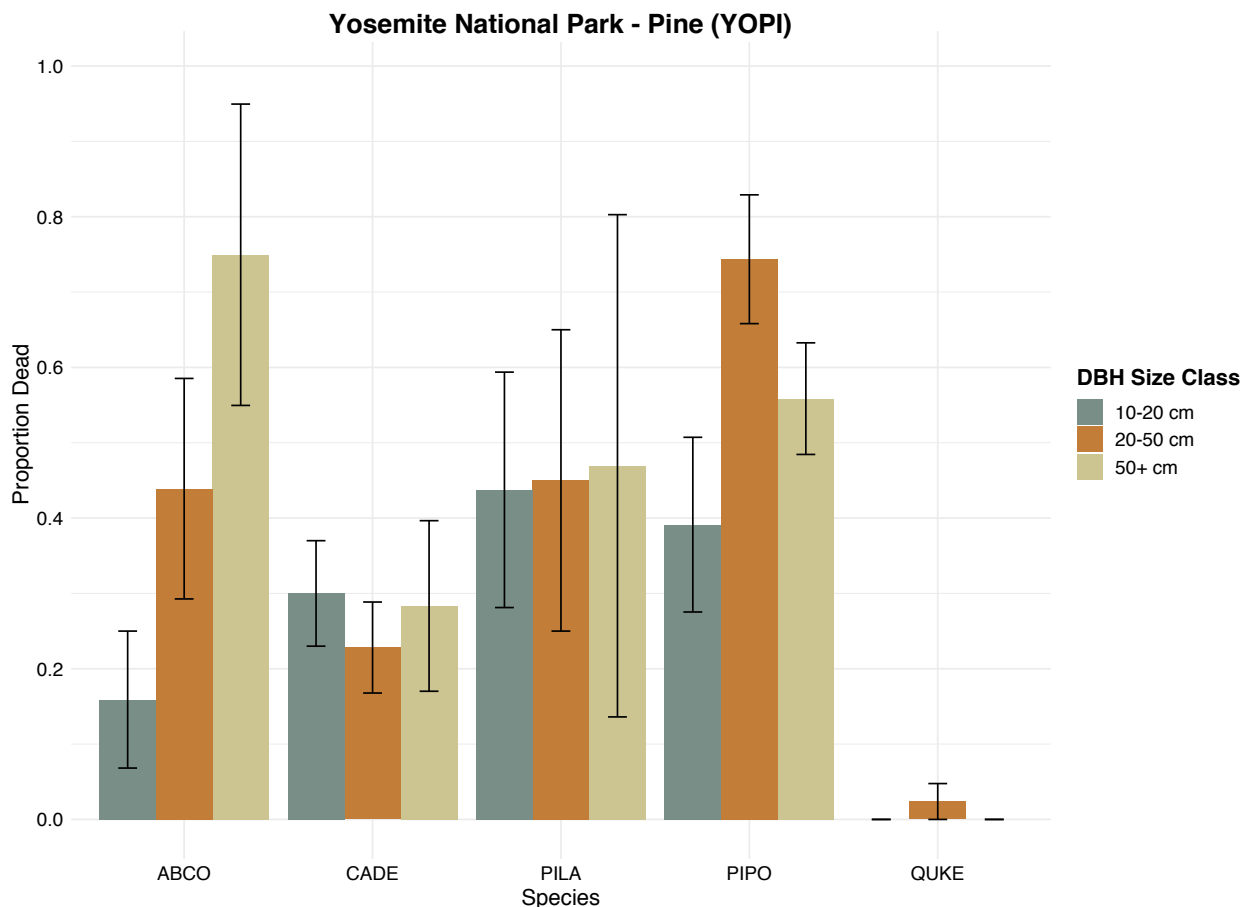


Figure 2. The proportion of recently dead trees in 2017 based on size class and tree species, where error bars represent the 95% confidence intervals (Drought Mortality Study, led by Axelson, Battles, and Kocher, written commun., Feb 2019). Species abbreviations on x-axis: ABCO = white fir; CADE = incense cedar; PILA = sugar pine; PIPO = ponderosa pine; QUKE = black oak.

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READY TO BURN: KNOBCONE PINE AND THE MYTH OF THE PHOENIX

Matthew Reilly

Of all the conifer species native to California, it is knobcone pine (*Pinus attenuata*) that most vividly invokes the image of a phoenix rising from the ashes. In ancient Greece, this mythological bird represented renewal, rebirth, and resilience. Likewise, botanists and fire ecologists in our region associate knobcone pine with the reinitiation of forest stands following high-severity fire. Like the phoenix, knobcone pine was born to burn. However, in stark contrast to the longevity, brilliance, and beauty of the mythological phoenix, knobcone pine is relatively short-lived and often exhibits slow, stunted growth forms, particularly in comparison to the stately stature and longevity of other conifers in California's forests. Despite the obvious and deceptively simple life history strategies associated with fire and serotinous tree species, the behavior of knobcone pine is far less predictable than one might assume. Indeed, the tree's opportunism and ability to colonize and adapt to many different environments means that its story is even more complex and nuanced than that of the phoenix.

SEROTINY: FIRE AS AN EVOLUTIONARY FORCE

Evidence of the role of fire as an evolutionary force in plants dates back as far as 350 million years. Serotiny is an ecological adaptation to fire in which plants store seeds in closed cones that reinitiate populations when a fire burns intensely enough to melt resins, open the cones, and trigger the release of seeds into post-fire environments that feature abundant light and reduced cover of surface litter (Lamont et al. 1991). The occurrence of serotiny in plant species around the world reflects the global role of fire in the evolution of plants. Levels of serotiny are particularly high in fire-prone regions of North America, South Africa, and Australia, but serotinous species are also found in the Mediterranean regions of Europe. Although knobcone pine may be the California species that most commonly evokes the image of the phoenix, it is far from the only conifer in our region that evolved this strategy. In North America, the diversity of serotinous conifers in California is unsurpassed.

The adaptive advantages of serotiny to plants that inhabit fire-prone regions such as California are clear [Figure 1]. Soon after fire, the cones of serotinous species such as knobcone pine open and release winged seeds, enabling rapid establishment and colonization of post-fire environments. As an ecological process, fire reinitiates succession and seral development. Exposure of bare mineral soil following the removal of litter and other accumulated dead organic matter facilitates germination and successful seedling establishment. By burning off the previously dominant vegetation, fire also increases light availability and increases the competitive advantages of post-fire colonizers that are intolerant of shade but capable of growing rapidly with more light. The existence of a "seedbank" on site means that seeds do not have to disperse long distances from the edges of large patches of tree mortality. Such rapid response makes serotinous species a key component of forest resilience to high-severity fire.

Evidence of serotinous conifers in California dates back as far as five million years ago during the late Miocene (Millar 1996). Researchers have hypothesized that more recently during the Pleistocene, approximately two million years ago, much of coastal and interior California was dominated by continuous forests consisting primarily of closed-cone pines



Figure 1. Knobcone pine with closed cones, open cones following fire, and post stand-replacing fire conditions (clockwise from top left). [Erik Jules]

(Axelrod and Cota 1993). During a warm period in the Holocene, the ranges of bishop pine (*P. muricata*) and Monterey pine (*P. radiata*), two of knobcone's closest relatives, contracted and ultimately retreated to geographically isolated pockets along the coast where they exist today in multiple disjunct populations. More recent research, however, suggests that the distribution of serotinous species may have been relatively stable over time (Millar 1999). These species may have responded to fluctuations in climate that alter the suitability of habitat and allow migration at shorter time scales. This perspective posits that during favorable periods, ranges expanded from geographically isolated refugia through colonization and establishment of new populations. During unfavorable periods, ranges contracted as populations that previously expanded into new habitats experienced high rates of local extirpation. This means that, over time, populations would blink on and off, effectively maintaining a biogeographic pattern characterized by many small and isolated populations, but potentially allowing for connectivity among populations.

Today, the serotinous conifers in our region fall within two genera, *Pinus* and *Hesperocyparis*, and all currently exist as isolated, disjunct populations. While the long-term history of expansion and contraction may remain a subject of debate, it is most likely that the current ranges of serotinous conifers are the most restricted they have been in recent centuries. As in many portions of the world, there is great concern that populations of fire-adapted species exist in a decadent state and are at risk of local extirpation from senescence due to 20th century fire exclusion management practices. As fire-free intervals approach the maximum lifespan of these trees, populations may blink out as individual trees age and die without releasing seeds. At the same time, increasing fire activity is prompting concern that short-interval, repeated, high-severity fire poses a risk to young stands before trees reach reproductive maturity. Both senescence and immaturity risk potentially pose a threat to biodiversity and forest resilience in our region. However, there is increasing evidence that the dynamics of serotinous species are more complex than the simple story of the phoenix, and that a major key to understanding the effects of contemporary fire regimes lies in broadening our knowledge of the ecological role of these species through a better understanding of their natural history.

NATURAL HISTORY AND ECOLOGICAL ROLE OF KNOBCONE PINE

Of all the serotinous conifers in California, knobcone pine is certainly the most ecologically wide-ranging and

geographically widespread [Figure 2]. Knobcone pine can be found at elevations upwards of 5,500 feet in cooler, moister montane environments, as well as below 1,000 feet in parts of its distribution in the coast ranges and in the hot, dry interior of California, where it is commonly found intermixing with chaparral vegetation. The heart of the species range lies in the Klamath Mountains of northern California and southwestern Oregon. Here, amidst one of the greatest diversity of conifer species in the world, knobcone pine thrives due to a history of frequent fire and a unique geological setting with an abundance of serpentine derived soils. The geographic distribution continues south where its range consists of smaller, isolated patches in the coastal ranges and the Sierra Nevada, and also includes a small disjunct population in Baja California, Mexico.

Knobcone pine has fascinated botanists in California for over a century now, and the recognition of its close association with fire dates back at least to the time of John Muir. In his 1894 book, *The Mountains of California*, Muir describes the species' life history and observes many of the characteristics that shape our understanding of knobcone pine (back then called

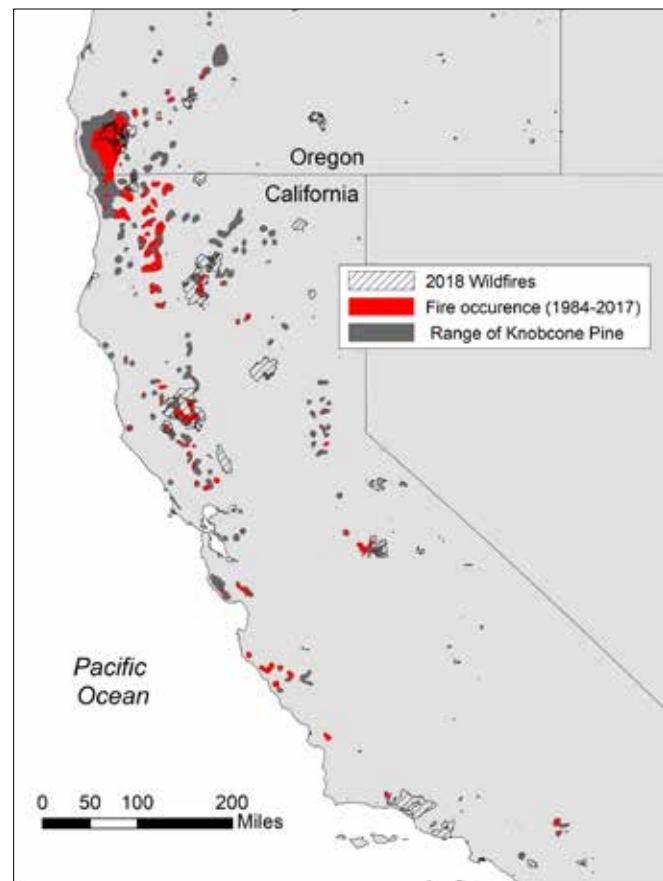


Figure 2. Range of knobcone pine in California and southwestern Oregon with perimeters of recent fires within its range. [Matthew Reilly]

Pinus tuberculata). He specifically describes the species as “curious” and “exceedingly slender and graceful in habit.” In a more scientific description, Muir astutely comments on the even-aged stand structure, conspicuous lack of regeneration, and what would seem to be a total reliance on fire for the discharge of seeds. In conclusion he states:

“I may at least call attention to the admirable adaptation of the tree to the fire-swept regions where alone it is found. After a grove has been destroyed, the ground is at once sown lavishly with all the seeds ripened during its whole life, which seem to have been carefully held in store with reference to such a calamity. Then a young grove immediately springs up, giving beauty for ashes.”

Although we don’t know of Muir’s familiarity with the mythological story the rising phoenix, it seems likely that he too would recognize the analogy.

In the years since Muir’s exploration, the life history of knobcone pine has received an increasing amount of scientific attention and observation. Like many serotinous conifers that inhabit landscapes subject to frequent wildfire around the world, knobcone pine matures to reproductive status at a relatively early age compared to most other conifers [Figure 3]. Trees may begin producing cones as early as four to 14 years of age. Early development of cones can help ensure persistence even when fire occurs extremely frequently, such as in the hot, dry Mediterranean summers of California. Most species that dominate landscapes shaped by frequent fire are adapted to low-severity fire and have thick bark and high canopies (e.g. ponderosa pine). However, knobcone pine thrives following intense, high-severity events. Lab experiments indicate that closed cones from knobcone pine require exposure to temperatures of 200°F for five minutes to open (Vogl 1973). As a tree ages, the number of cones increases and the tree can continue producing viable seed past 70 years (Fry and Stephens 2013). Thus, a single old tree may contain hundreds of cones in the canopy and along the bole of the tree. Provided that a fire does occur, these legacy trees can essentially provide an in-situ seedbank to recolonize following such an event. Conversely, in the absence of fire, populations may ultimately decline and senesce as individual trees age and die.

Rapid early growth and prolific cone production in knobcone pine are not without their costs, however. Rapid growth when conditions are open and relatively free of competition may weaken trees and leave them prone to insects and disease later in life. Thus, trees often exhibit poor growth form as they age. Age-related decadence is readily apparent in trees 75 years and older. Although some individuals may live more than 90 years, most trees rarely live more than 80 years (Howard 1992). The lack of longevity in knobcone pine leaves populations prone to risk of local extirpation when fire return intervals are long relative to their lifespan. Despite the available information on many aspects of the life history of knobcone pine, most current knowledge comes from relatively few study sites scattered across its range. There is little known about geographic variability in growth, maximum age, time to maturity, or seed viability across the broad range of environments it occurs in.

HEDGING BETS THROUGH PARTIAL SEROTINY

Much of the scientific work on knobcone pine has focused on its serotinous nature, given its status as one of the conifer species where serotiny is most strongly expressed. However, many serotinous species exhibit partial serotiny, where cones may open in the absence of fire in at least some portions of their range. For example, lodgepole pine (*P. contorta*), North America’s most well-known and widespread serotinous species, is variably serotinous across the northern Rocky Mountains, and primarily non-serotinous throughout its range in California. For many species, partial serotiny is thought to be a bet-hedging strategy in the face of variable and unpredictable fire return intervals. Many serotinous species exhibit necrisence, or the opening of cones, upon the death of an individual. Cones on some species may also open during drought conditions, a behavior referred to as xeriscence. Such behavior may accelerate cone opening and seed release, especially in portions of a species’ range where serotiny is weak or variable. However, successful regeneration in these situations is far less likely than following fire, when establishment is

Figure 3. Knobcone pine regeneration near the North Fork of the Smith River shows trees producing cones 13 years following the Biscuit Fire. [Matthew Reilly]



Figure 4. Partially serotinous cones on a young knobcone pine 13 years after the Biscuit Fire near the North Fork of the Smith River.

[Matthew Reilly]

optimized by the exposure of mineral soil and reduction in shade and competition.

Knobcone pine exhibits partial serotiny across some portions of its range [Figure 4], but extremely little is known about how the degree of serotiny varies with age or geographically across its range. Xeriscence and necriscence may facilitate invasion of habitats where thin soils limit vegetation density, light levels are relatively high, and leaf litter is thin. Thus, it seems likely that partial serotiny provides an alternative pathway for the species' persistence and expansion in the absence of fire, particularly into woodlands or ecotonal areas between forest and non-forest vegetation types such as shrublands or chaparral or meadows [Figure 5].

IMPACT OF CHANGING FIRE REGIMES

Forest managers are concerned that many populations of fire-adapted species currently exist in a decadent state and are at risk of local extirpation due to fire exclusion during the 20th century. Studies from all over the world, including Australia, South Africa, and the eastern United States, show mature and ageing populations of serotinous species. Likewise, studies of knobcone pine in areas such as the Mayacamas Mountains in the inner coast ranges of southeastern Mendocino and western Lake Counties, the Santa Ana mountains on the south coast, and inland populations in the southern Cascades, suggest that this species is also at risk of senescence across much of its range. Recent research indicates that during the early 2000s, mature and old-growth populations of knobcone covered approximately 75% of its range (Reilly et al. 2019). Such dominance of mature and old-growth stands suggests the potential for widespread extirpation across the range as decadent trees approach their maximum lifespan and senesce. Such extirpation is linked not only to the death of mature trees, but also to the loss of an in-situ seedbank for future recruitment. Loss of serotinous species such as knobcone pine is a threat to biodiversity and could reduce stand and landscape resilience to future fire.

The prevalence of decadent populations of knobcone pine is consistent with what fire ecologists have begun referring to as a “fire



Figure 5. Knobcone pine encroaching an unburned mature sugar pine woodland in the Klamath Mountains. [Matthew Reilly]

deficit” due the fire exclusion management practices of the last century. Historically, fire return intervals across the range of knobcone pine ranged from 10 to 25 years in forested landscapes and perhaps up to 70 years in shrub and chaparral dominated landscapes (Van de Water and Safford 2011). Between 1950 and 1985, however, less than 5% of the range of knobcone pine experienced fire (Figure 6). However, since in the mid-1980s we have observed a steady increase in the annual area burned across the range of the species, so that between 1984 and 2015, fires burned approximately 40% of the range. Several fires in particular burned large portions of the knobcones' range in northern California and southwestern Oregon (i.e. the 1987 fires in the Klamath Mountains and the 2002 Biscuit Fire affecting 490,000 acres). This trend has continued in recent years with the economically and socially devastating Mendocino Complex fires (~450,000 acres) and Carr Fire (230,000 acres) in 2018. These and others fires burned approximately 13% of the species' range last summer [Figure 2]. Recent fires have reinitiated populations and promoted a cumulative expansion of the species though colonization of new sites in many parts of the species' range (Reilly et al. 2019).

In light of rapidly changing disturbance regimes in many regions around the world, the risk of repeated fires

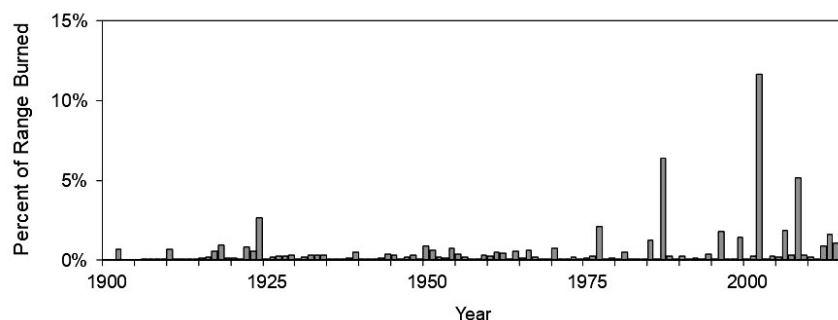


Figure 6. A century of fire history across the range of knobcone pine. [Matthew Reilly]

occurring at short intervals has garnered significant scientific attention. This phenomenon, frequently referred to as “immaturity risk” or the “interval squeeze,” happens when repeated fires occur at intervals shorter than the time it takes for trees to reach reproductive maturity and start producing cones. Multiple case studies demonstrate reduced regeneration of knobcone pine and other serotinous species following repeated short interval fires. In one of the most extreme cases, approximately half of the range of *Banksia hookeriana*, a serotinous shrub in Australia, burned in a single 117,000 hectare fire; seven years later another fire burned part of that range and resulted in local extirpation of the species (Enright et al. 1996). Although repeated fire at an interval of less than 10 years (a conservative estimate of time to maturity in knobcone pine) affected less than 1% of the entire species’ range up until 2015, in recent years the increasing frequency of fire and the occurrence of multiple large fires mean that immaturity risk will increase in the immediate future. In addition to the above-noted concerns surrounding the local extirpation of serotinous species due to immaturity risk, there is also the potential for conversion from forest to non-forest conditions.

CONCLUSIONS

It seems inevitable that despite the effects of 20th century fire exclusion, knobcone pine will continue its role as a phoenix of the forest, given projections of drier summers and increased fire activity into the 21st century. However, understanding the effects of contemporary fire regimes on knobcone pine and its distribution is far more complex than initially considered. In the absence of fire, knobcone pine may face the risk of local extirpation across certain portions of its range, particularly where forests are more productive and competition with longer-lived species may increase the knobcone pine’s risk of senescence. On serpentine soils and in hotter, drier portions of its range, knob-

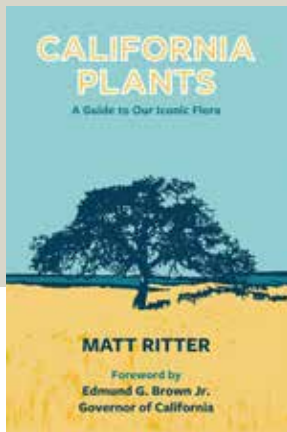
cone populations may have the potential to persist for longer and expand into chaparral or other non-forested vegetation types in the absence of fire through partial serotiny [Figure 7]. Forecasting the future role and health of knobcone pine will depend on developing a better understanding of the adaptive capacity of the species, as well as a more nuanced characterization of its basic life history and how it varies across its range.

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Figure 7. A self-perpetuating population of knobcone pine? On Gasquet Mountain near the Smith River in Northern California, a stand of knobcone pine dominates a southwestern slope that burned in 1950. Dead and dying trees are widespread and intermixed with regenerating saplings. [Matthew Reilly]





California Plants: A Guide to Our Iconic Flora

by MATT RITTER

Pacific Street Publishing, San Luis Obispo, CA. 321 pp.
ISBN: 978-0-9998960-0-6. \$27.50 (paperback)

Matt Ritter's *California Plants: A Guide to Our Iconic Flora* is a welcome introductory guide to California's extraordinary flora, well-suited to college students of all levels and to the general plant enthusiast, while also being an enjoyable read for the seasoned botanist. The book, which is sized small enough to be carried into the field, has an attractive design combined with accessible prose describing some 500 species and featuring more than 1,000 high-resolution photos.

The relevance of Dr. Ritter's book is found within the first pages in the forward written by former Governor Jerry Brown, a timely contribution in light of Brown's September 2018 California Biodiversity Initiative (California Biodiversity Action Plan 2018), which carefully lays out "A Roadmap for Protecting the State's Natural Heritage," especially California's plant life.

The opening statement of the book—"California is one of the world's few biodiversity hotspots"—prepares the reader for the richness of the seven broad vegetation types that the author uses as his organizational framework. These are: shrubland plants, wildflowers and grassland plants, forests and woodlands, coastal plants, marsh and wetland plants, desert plants, and lastly, non-native plants. As you can see, *California Plants* is oriented around the state's more common—and broadly defined—habitat types; there surely are others that might have been included, but the book is aiming to be useful more than comprehensive. Indeed, the book focuses on covering the more common and widespread plants, and does not attempt to address every single species found in our large and diverse state. In some cases, genera rather than species are covered, as with manzanita (*Arctostaphylos*). And of course, this is not the only book one should read to understand California plants; fortunately, the volume includes a list of other useful books and online resources for further study.

The introduction to each vegetation group includes a brief narrative about the variations within that vegetation type. For example, the shrubland chapter covers species in woody chaparral and coastal scrub communities; the forest and woodland chapter covers species in oak savannah woodlands, montane forests and riparian woodlands; etc. Within each section, the plants are listed alphabetically by Latin name, a potential challenge for the introductory user.

Most of the species (or genera) covered get their own full-page treatment, with a photo, range map, a common name, the Latin name (with pronunciation guide!), and a short narrative description that highlights some of the plant's main characteristics, often including morphology, ethnobotanical and medicinal properties, plant associations, and botanical history.

All told, *California Plants* is an attractive additional resource for those Californians already botanically inclined, and a fine introduction for those just beginning their exploration of the state's rich native flora.

—BRETT HALL.

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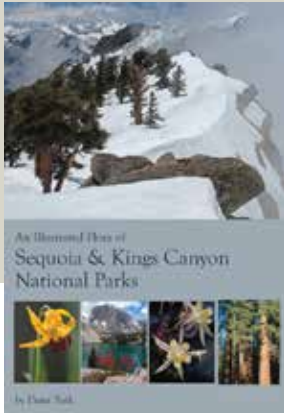
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An Illustrated Flora of Sequoia and Kings Canyon National Parks

by DANA YORK

Backcountry Press & California Native Plant Society. 576 pp.

ISBN: 978-0943460611 \$39.95 (paperback)

What better treat could there be for the botanically-inclined person than to have a new flora published for the area where you live? Dana York's new book, *An Illustrated Flora of Sequoia and Kings Canyon National Parks and Adjacent Southern Sierra Nevada*, is the first ever comprehensive guide to the plants of these two majestic national parks and their adjacent areas (primarily the entire montane region to the west of Kings Canyon National Park).

This book is best suited for those familiar with plant identification using dichotomous keys, rather than the typical park visitor. That said, the keys, descriptions, and overall format are refreshingly simple, making it easy enough to be useful to the budding plant enthusiast as well as the professional-level botanist. Mr. York presents just enough information in the keys and descriptions to distinguish the plant you are trying to identify from others in the region. The book, which covers some 1,800 species and varieties, is organized by the familiar taxonomic grouping of major monophyletic groups or clades for vascular plants, then by family, genera, and taxon. The keys and descriptions do not use unnecessarily technical terms, and a simple glossary is provided in the back.

A nice feature of the book is the illustration of the plant and its distinguishing features that accompanies each plant description. The only downside is that the drawings are copies from other books and, as such, are sometimes not as sharp as I would like, especially for some of the sedges and grasses.

The book is available in print or as an e-book, with the e-book being a convenient alternative to carrying a hefty volume into the field. And, of course, the e-book can be more easily updated to reflect the latest taxonomic and nomenclatural changes. Indeed, less than a year since its release, the Kindle version is already in its seventh edition.

Overall, this book is a wonderful compilation of the richly diverse flora of the region, making identification much easier for anyone botanizing in Sequoia and Kings Canyon National Parks.

An Illustrated Flora of Sequoia and Kings Canyon National Park can be purchased for \$39.95 from the CNPS online store (store.cnps.org), and the e-book is available from Amazon. [Note: the e-book version has hyperlinks and will not work on the Kindle Paperwhite, but is compatible with Kindle Fire or the Kindle app on a phone or tablet.]

—ANN HUBER, *Plant Ecologist,
Sequoia & Kings Canyon National Parks*

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IN MEMORIAM: JO KITZ, CHAMPION OF THE SANTA MONICA MOUNTAINS

By Steve Hartman

Environmental advocate and native plant conservationist Jo Kitz, who earned awards for her work with the California Native Plant Society (CNPS) and other conservation organizations, passed away on September 2, 2018 in Boise, Idaho. She was 86 years old. Born in the British West Indies in 1932, Jo moved with her family to Portland, Oregon during World War II. There, she loved spending time in the forests around Mount Hood. Her family later moved to Louisiana, where she attended Louisiana State University. She received her Bachelor of Arts degree from Reed College in Oregon in 1954 and married Bill Kitz, a Navy pilot, in 1955. In 1959, they settled in the San Fernando Valley where Jo resided for 60 years and raised her two children, daughter Jamie and son Kevin.

Jo began her career as an elementary school teacher but found her true passion when she began volunteering for the Sierra Club in the 1960s. Her work to raise awareness of the beauty and benefits of the Santa Monica Mountains significantly contributed to the creation of the Santa Monica Mountains National Recreation Area in 1978. In 1989 she joined the Mountains Restoration Trust where she served as Program Director until her retirement in 2012. Her work to introduce Los Angeles residents to the Santa Monica Mountains included “Sundays in the Santa Monicas”—a program that raised awareness of the natural values of the mountain range by offering walks and hikes to residents and visitors.

Jo held volunteer leadership positions in several other environmental and conservation organizations. She was instrumental in the formation of the California Invasive Plant Council (Cal-IPC), a nonprofit organization dedicated to curbing the spread of invasive plants across California. Jo led countless volunteers from church groups, school groups, and at-risk youth groups to remove invasive weeds and replace them with California native plants, earning the cherished nickname of “Intrepid Weed Warrior.”

Jo became active in CNPS in the 1970s and was an important presence in the Los Angeles/Santa Monica Mountains chapter for many years, including serv-



Jo Kitz demonstrates invasive plant removal strategies on a field trip at a 2004 Cal-IPC symposium in Southern California. [Doug Johnson]

ing several years as chapter president. Her volunteer efforts for CNPS are documented in a 1995 article in *Fremontia* (Vol. 23, No. 2) after she was named as a Fellow, CNPS's highest honor. Jo also served as a board member for statewide CNPS. In the local chapter, she handled plant and book sales for many years, and gave her time generously for special projects. In 1992, she started a program to restore the oak woodlands of Malibu Creek State Park. Under her leadership, volunteers planted more than 2,000 native oak trees and dedicated thousands of hours to keeping them alive.

Linda Hardie (past LA/SMM chapter president) worked with Jo in 1984 to co-edit Nancy Dale's *Flowering Plants of the Santa Monica Mountains*. Linda says, “Jo was not only a strong leader in the Santa Monica Mountains, but she was also a strong team player as well as a mentor to many of us. It was a privilege to work with Jo and a gift to become her friend.”

In 2004, California Assemblywoman Fran Pavley honored Jo Kitz as a “Woman of the Year” in a ceremony at the California State Capital. The members of CNPS join with hundreds of others whose lives she touched in celebrating the life and achievements of this remarkable woman warrior for the landscapes of Southern California.

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