MANZANITA

Volume 25, No. 4, 2021/Volume 26, No. 1, 2022 • Published by the Friends of the Regional Parks Botanic Garden

Whitebark Pine In California

by Michael Kauffmann

Introduction

Whitebark pine (*Pinus albicaulis*) is a true summit tree that survives in only the highest subalpine conditions. This species defines the extreme limits of the timber across California. From vast stands stretching across the contiguous high elevations of the Sierra Nevada and Warner Mountains to the individual summits, or sky islands, of the Cascades and Klamath Mountains, whitebark pine represents an aesthetic splendor that rivals the finest subalpine scenery of the West. Scraggly branches splay about in the windward direction—where often just as many are dead as alive. Trees are strategically scattered across the landscape, sculpted specifically by the meager conditions offered. Centuries of slow growth are in strict compliance with the rigorous demands of sun, soil, water, and wind. Their multitude of charismatic individual forms, whether on select summits or within vast stands, exhibits a deep-time aptitude for life.

Sun-bleached whitebark pine skeleton in the Klamath National Forest.

California is unique in having the greatest variety of habitats and ecological settings where whitebark pine thrives. The most extensive stands are in the central and southern portions of the Sierra Nevada. To the north, as the Sierra Nevada transitions to the Cascade Range in Lassen County, whitebark pine occurs on volcanic summits from Lassen Volcanic National Park to Mount Shasta (these two areas hold the two largest stands in the Cascades) as well as on other volcanic summits of high-elevation mountains. Near the borders of California with Nevada and Oregon, the species inhabits high elevations of the Great Basin in the Warner Mountains. Finally, but importantly, there are isolated stands of whitebark in the Klamath Mountains; these sky islands are

MANZANITA

Volume 25, No. 4, 2021/Volume 26, No. 1, 2022

IN THIS ISSUE:

Western redcedar (*Thuja plicata*). Emerald Canary

BOTANIC GARDEN STAFF

Director: Bart O'Brien
Botanic Garden Supervisor: Liz Bittner
Gardeners: Ben Anderson, Gideon Dollarhide, Marcus Tamura, Michael Uhler
Administrative Specialist: Angelina Manno
Interpretive Student Aides: Calvin Miller, Diana Wahl

FRIENDS PUBLICATIONS COMMITTEE

Publications Chair: Rosie Andrews
Managing Editors: Allison Kidder and Rosie Andrews
Copyeditor: Doris Kretschmer
Graphic Designer: Emerald Canary
Editor, ***The Botanic Garden Monthly***: Alicia Springer
Maggie Ingalls
Bart O'Brien
Alicia Springer
Douglas Stimpson
Susan Wijeyesekera

MEMBERSHIP

Your membership in the Friends of the Regional Parks Botanic Garden supports the important work of the Garden in educational programs, conservation, and horticultural experimentation. Funds raised by the Friends help provide long-term financial security for the Garden as well as new facilities and programs.

GENERAL

Individual $50 Limited Income/Student $30 Family/Dual $75

SPECIAL GARDEN FRIEND

California Poppy $125
Buckwheat $250
Ceanothus $500
Manzanita $1000

Members receive *Manzanita*, a quarterly publication of the Friends, as well as discounts on classes and field trips offered by the Friends, discounts at nurseries listed on the back cover, and early admission to the Garden's plant sales. Friends members gain free admission to participating gardens through the American Horticultural Society's Reciprocal Admissions Program. Contact the individual garden to verify this benefit.

FRIENDS OF THE REGIONAL PARKS BOTANIC GARDEN

FRIENDS LEADERSHIP COUNCIL

Rosalie Gonzales, Co-Chair
David Sherertz, Co-Chair
Rosie Andrews
Renee Cheney-Cohen
Bob Finkel
Roz Hardy
Liz Horowitz
Pattie Litton
Ingrid Madsen
David Savidge
Susan Wijeyesekera

GIFTS AND ENDOWMENTS

Donations to the Friends are welcome and may be designated for special projects or given in honor or in memory of someone. Contributions to the Regional Parks Botanic Garden Endowment Fund assist in providing financial security for the Garden. Please make all checks payable to the Regional Parks Foundation; note whether for Friends membership, gift, or Endowment Fund; and send to:

Friends of the Regional Parks
Botanic Garden
P.O. Box 7551
Berkeley, CA 94707

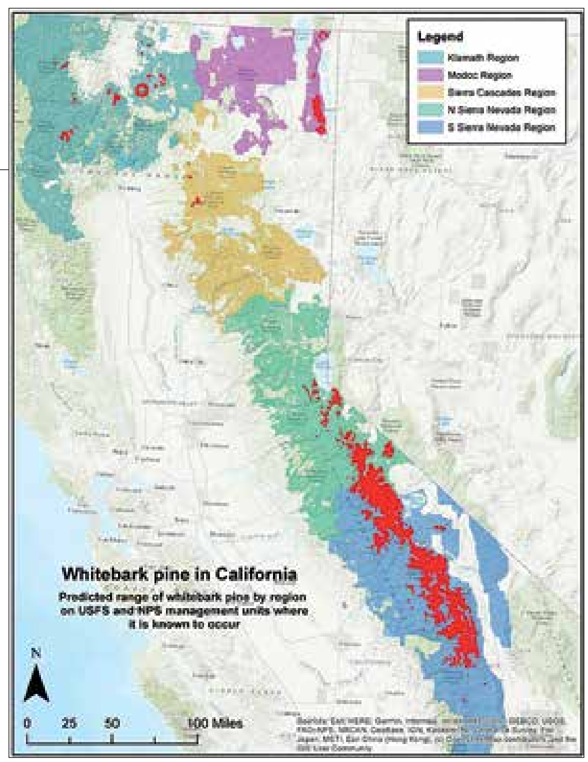
Friends volunteers develop and oversee many of the Garden's educational offerings and its website, produce the *Manzanita*, and much more! New volunteers are always welcome.

For information about the Friends, membership, and becoming a Garden volunteer or docent, contact info@nativeplants.org, visit www.nativeplants.org, or call 510-544-3169.

scattered across the diverse geological landscape of northwest California. Given this vast diversity in landscape and in scale, this article confines itself to the specific biology, ecology, distribution, and threats to whitebark pine within California.

The US Fish and Wildlife Service designated whitebark pine as Threatened under the Endangered Species Act in 2020 due to the impacts of a suite of factors including altered fire regimes; the introduced pathogen, white pine blister rust (*Cronartium ribicola*); mountain pine beetle (*Dendroctonus ponderosae*); and climate change (Tomback and Achuff 2010, Slaton et al. 2019b). Decimation of populations in the northern Rocky Mountains led to Canada listing the species as endangered in 2010. As one of only a few trees in California's highest mountains, whitebark pine is a keystone species, providing crucial ecosystem services at these high elevations. Current and potential losses of this species pose serious threats to biodiversity in these unique settings.

Western North American range map for whitebark pine (*Pinus albicaulis*) from *Conifers of the Pacific Slope*, Michael Kauffmann 2013.



Kendra Sikes, CNPS

California range map for whitebark pine indicated in red, across four ecological regions.

Biology and Ecology

Taxonomy

From a distance, whitebark pine might be confused with lodgepole or western white pine. The bark is like that of lodgepole pine, but lodgepole has only two needles per bundle while whitebark pine has five. The needles are like those of western white pine, but the whitebark form is bushier at the branch tips, cones are smaller and shorter, and the bark is less furrowed and blocky. Slaton et al. (2019) point out that you can distinguish western white pine in the field with a hand lens by noting the fine serrations on its needle-like leaves; they also explain that limber and whitebark pine are virtually indistinguishable, especially when young, before whitebark acquires its namesake color and develops mature cones.

Distribution

Within California, whitebark pines are found as outliers of their much broader range to the north. Of the approximately 378,693 acres mapped where whitebark pine forms pure stands in California, >99% of the acreage is on public land, often in remote wilderness settings of National Forest and National Park lands; however, the acreage of whitebark pine in mixed stands across the state is much greater and has not been thoroughly mapped at this point. The majority of whitebark pine-dominant stands are located within the National Forests in the Sierra Nevada Region (~83%). Approximately ~7% are found in the California Cascades (Mount Shasta and Lassen Peak), ~8% in the Warner Mountains, and ~2% in the Klamath Mountains.

The species prefers cold, windy, snowy, and generally moist zones. In the moist areas of the Klamath and Cascades, it is most abundant on the warmer and drier sites. In the more arid Warner Mountains and in the Sierra Nevada, the species prefers the cooler, more mesic, north-facing slopes. However, some of these patterns are shifting. In the last 50 years, whitebark pines have been able to colonize novel habitat released by human-induced climatic changes, including north-facing slopes that are now snow-free earlier in the year as well as lower elevations that have been subjected to browsing regimes by sheep, particularly in the Warner Mountains (Kauffmann et al. 2014).

Plant-Animal Interactions

Unlike other five-needle pines, the cone of whitebark pine does not open at maturity, and its seed is "wingless" and rarely dispersed by wind. Whitebark pine relies on dispersion by squirrels or birds, primarily Clark's nutcrackers (*Nucifraga columbiana*), for seed distribution and future seedling recruitment (Arno and Hoff 1989, Tomback et al. 2001). The birds open the cones, collect the seeds, and bury small caches in the soil; if not reclaimed, the seeds may germinate and grow. Because of this, regeneration is most often in clumps, a form that can be accentuated by the tendency of lower branches to become pressed horizontally against ground moist from snow and then grow upright. Stems that do reach tree size of greater than three inches in diameter at breast height (DBH) are generally small compared to most other conifers, with height and diameter averaging 23 feet and eight inches, respectively, in California (US Forest Service unpublished data).

Justin Garwood

Clark's nutcrackers and whitebark pine in the Trinity Alps Wilderness.

Over time, this relationship with Clark's nutcracker has developed into what is termed keystone mutualism (i.e., the two species are dependent on each other). In Arizona, Stephen Vander Wall and Russell Balda estimated the combined caching ability for a flock of 150 jays to be several thousand seeds per acre, totaling nearly 4 million seeds per flock, with the combined nutritional value equivalent to 650 pounds of fat (Lanner 1996). Four pounds of fat per bird is significant nutrition for individuals weighing less than 5 ounces. Inevitably around 20% of the seeds are unused or moved by other animals and, in the years following, clumps of whitebark pine saplings grow from these remaining caches. This mechanism of dispersal is important for both range expansion and genetic diversity across California.

Fire Ecology

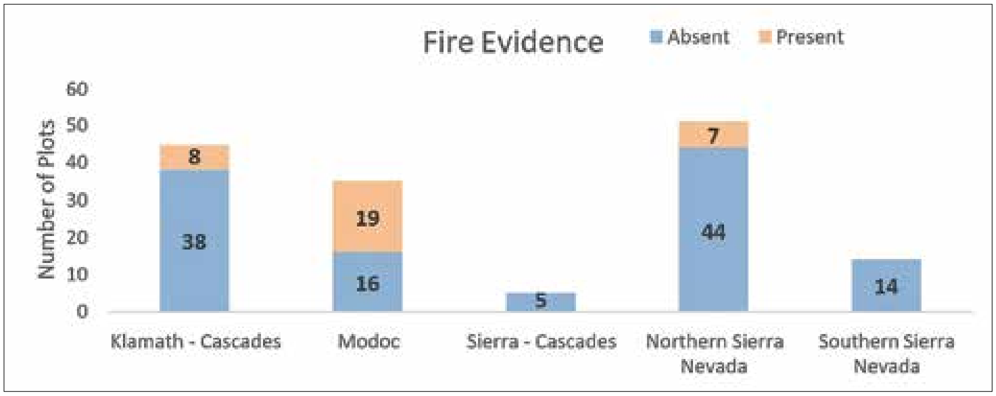
Slaton et al. (2019) stress that fire plays an important role in the health and resilience of whitebark pine forests. Approximately every 70 to 90 years, fires return in upright stands (though not in the wind- and snow-stunted, low-growing krummholz), although shorter fire-return intervals have been documented in other high-elevation forest types (Murray and Siderius 2018). With variability in both frequency and intensity, effects from fires are also variable. California's forests are experiencing shifts in fire severity, frequency, and extent due to warming temperatures, fire suppression, fuel accumulation, and human ignitions (Keeley and Syphard 2016).

In productive areas in some parts of whitebark pine's range, fire exclusion at high elevations has led to replacement by a variety of other conifers. Burning eliminates competitive shade-tolerant trees while encouraging open and complex habitat preferred for caching by Clark's nutcracker (Keane et al. 2012). In California, whitebark pine is encroached on mainly by red fir (*Abies magnifica*) and mountain hemlock (*Tsuga mertensiana*) in the northern part of the state. Other conifers less commonly encroaching on whitebark pine habitat include white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*). We are just beginning to learn about the extent of fire impacts on California's whitebark pine stands, and high intensity fires are increasing within whitebark pine stands in California.

California Vegetation Patterns

Klamath Mountains

In California's Klamath Mountains, whitebark pines are true summit trees that survive in only



Fire evidence in whitebark pine stands across California by region, per data collected by CNPS and Michael Kauffmann in 2013 and 2018.

Melissa DeSiervo

Burned whitebark pines in the 2014 Whites Fire, Russian Wilderness, Klamath National Forest.

the highest subalpine conditions, where they define the limits of timber line at 7,000-9,000 feet on localized mountain tops (known as sky islands). Trees are often sparingly scattered across xeric serpentine savannahs or take purchase in meager soil deposits between granite outcrops where centuries of slow growth are in strict compliance with the rigorous demands of sun, soil, water, and wind. In the lower extent of the range, whitebark pines form complex vegetation communities in peripheral areas, including edges of lakes or meadows where they are less likely to be impacted by competition from other species. Oregon's Klamath Mountains hold only one small, scattered collection of fewer than 10 trees near the summit of Mount Ashland.

Klamath Mountain vegetation patterns

Because of the average lower elevation of Klamath Mountain whitebark pine stands compared to those in the rest of California, unusual distribution patterns have developed. Most whitebark pine grows on south-facing slopes due to competition from firs and hemlocks on north slopes. Because of complex soils, vegetation associates are diverse, and often include endemic species from between subregions.

The most extensive whitebark pine stand in the Klamath Mountains is around the summit of Mount Eddy (9,026 feet), the highest peak in the range.

Tree associates here, within one of the most species-rich temperate conifers forests in the world, include Klamath foxtail pine (*Pinus balfouriana* subsp. *balfouriana*), western white pine, white fir, Shasta fir (*Abies magnifica* var. *shastensis*), mountain hemlock, subalpine fir (*Abies lasiocarpa*), common juniper (*Juniperus communis* var. *saxatilis*), and Douglas-fir. Brewer spruce (*Picea breweriana*) or Pacific yew (*Taxus brevifolia*) are rarely found with whitebark pine. Unlike in California's Cascades, Sierra lodgepole pine (*Pinus contorta* subsp. *murrayana*) is an uncommon associate in the Klamath Mountains. When present, white and Shasta fir, along with mountain hemlock, are typically seedlings or saplings that appear to have been pioneering (encroaching on) whitebark pine habitat in the last 50-100 years due to a combination of decreased snowpack, fire suppression, and a lengthening growing season.

Shrub associates on granites of the Trinity Alps and Salmon Mountains (Klamath sub-ranges) include western moss heather (*Cassiope mertensiana*), pinemat (*Ceanothus prostratus* var. *prostratus*), tobacco brush (*Ceanothus velutinus*), Sierra laurel (*Leucothoe davisiae*), and huckleberry oak (*Quercus vacciniifolia*). In the eastern Klamath on the ancient ultramafic soils, understory associates include curl leaf mountain mahogany (*Cercocarpus ledifolius* var. *intermontanus*), shrubby cinquefoil (*Dasiphora fruticosa*), rabbitbrush species including *Ericameria greenei*, *Ericameria nauseosa* var. *speciosa*, and *Ericameria parryi* var. *latior*, Oregon boxwood (*Paxistima myrsinites*), and dwarf bilberry (*Vaccinium cespitosum*).

California's Cascade Range

In the Cascade Range, whitebark pine occurs in a narrow belt of small, disjunct populations on the summits of volcanoes in the north-central part of California, from the California-Oregon border east of Interstate 5 southward to Lassen Volcanic National Park. Across the Cascades they grow at elevations between 7,500 and 12,000 feet. In the lower elevations, trees become quite large (2-4 foot DBH) and tall (60-80 feet). At the upper elevation limits, krummholz individuals approach the true alpine zone on Mount Shasta and the extreme subalpine zone on Mount Lassen. The only true alpine zone in California is on the summit of Mount Shasta.

In the Lassen area, there are three separate populations of whitebark pine, isolated on the highest peaks and subalpine landscapes, where they range from approximately 7,000 to 10,000 feet elevation. One of these populations is located around the Lassen Peak highlands within Lassen Volcanic National Park, managed by the National Park Service. Two other populations occur in the Lassen National Forest. One is within the Thousand Lakes Wilderness around Magee and Crater Peaks. This stand occurs along the rim of the ancient Thousand Lakes Volcano, which has eroded away. The other is a scattered stand of approximately 40 trees across 15 acres on the summit of Burney Mountain.

Cascades vegetation patterns

Whitebark pine occurs with other conifers, including white fir, Shasta fir, mountain hemlock, lodgepole pine, and western white pine. Mountain hemlocks are commonly either pioneering or encroaching within, or adjacent to, stands of whitebark pine. This pattern is easily seen in Lassen Volcanic National Park along the Bumpass Hell Trail. In the swales carved out by erosion, decreased snowpack (and early season melting) has led to novel habitat in which hemlocks are rapidly pioneering. This is allowing encroachment into whitebark pine habitat on the ridges above these swales.

Another interesting pattern seen in the upper reaches of tree line on Mount Shasta is the ecological release whitebark pines are experiencing. What were formerly krummholz trees are now sending leaders skyward. This is most likely occurring due to decreased snowpack and early season melting. With the ability to explore a longer growing season, krummholz whitebark pines are becoming upright trees.

Common shrubs include Rocky Mountain maple (*Acer glabrum* var. *glabrum*), pine mat manzanita (*Arctostaphylos nevadensis*), greenleaf manzanita (*Arctostaphylos patula*), pinemat (C*eanothus prostratus* var. *prostratus*), tobacco brush (*Ceanothus velutinus*), Sierra chinquapin (*Chrysolepis sempervirens*), showy rabbitbrush (*Ericameria nauseosa* var. *speciosa*), marum-leaved buckwheat (*Eriogonum marifolium*), and western blueberry (*Vaccinium uliginosum* subsp. *occidentale*).

California's Warner Mountains

In northern California's Great Basin, whitebark pine only occurs in the Warner Mountains. This fault-block range runs north to south for approximately 80 miles. The highest average elevation is in the south, and is mostly protected within the South Warner Wilderness. North of Highway 299, small stands of whitebark pine persist sporadically, with the largest stands near the Oregon border along Mount Bidwell's extensive ridgeline. The area between Mount Vida (8,240 feet) north to Mount Bidwell (8,266 feet) hosts scattered stands of whitebark pine. Large swaths of conifers, including lodgepole, western white, and whitebark pine, were devastated by mountain pine beetles in the mid- to late-2000s. While many of the larger trees died, sapling and seedling regeneration is vigorous, and the short-term future of pines appears promising.

Whitebark pine scattered in the ancient crater of the Thousand Lakes Volcano, now within the Thousand Lakes Wilderness, Lassen National Forest.

Near the highest point in the Warner Mountains, Eagle Peak (9,892 feet), ancient whitebark pines grow above the Surprise Valley in the Modoc National Forest.

The small populations of whitebark pine in the central Warner Mountains exhibit excellent health on and around Bald Mountain (8,274 feet) and Cedar Mountain (8,152 feet). Stand size is small, and the trees are geographically isolated, thus mountain bark beetles were not present during the outbreaks between 2005-2009.

Large and extensive stands of whitebark pine exist in the southern Warner Mountains. Much of this population is protected within the South Warner Wilderness highlighted by Eagle Peak (9,892 feet). Across this high-elevation escarpment whitebark pine dominates the highest elevations and mixes with lodgepole pine in the mid- to upper-elevations. Large pockets of lodgepole pine and smaller pockets of whitebark were killed by mountain pine beetles in the 2005-2009 outbreak. North-facing slopes of the highest elevations are being pioneered by young seedlings due to decreased snowpack. The seedlings began recruiting (establishing themselves) 20-40 years ago and are rapidly expanding in this novel habitat. A smaller, somewhat disjunct stand defines the southern limit of whitebark in the Warner Mountains around Emerson Peak (8,989 feet). Whitebark pine is common here on north-facing slopes where patterns of mountain bark beetle mortality and recruitment are similar to that seen in the northern Warner Mountains near Mount Bidwell. The species is expanding into the lower elevations in grazed areas, most likely due to decreased competition from shrubs, which are consumed by herds of grazing sheep.

Warner Mountain vegetation patterns

Conifer associates include white fir, western white pine, lodgepole pine, and the rare mountain hemlock. Common shrubs include pine mat manzanita, low sagebrush (*Artemisia arbuscula* subsp. *arbuscula*), mountain sagebrush (*Artemisia tridentata* subsp. *vaseyana*), rayless goldenbush (*Ericameria discoidea*), Greene's goldenbush (*Ericameria greenei*), ocean spray (*Holodiscus discolor* var. *glabrescens*), tobacco brush, antelope bush (*Purshia tridentata*), mountain snowberry (*Symphoricarpos rotundifolius*), and others.

California's Sierra Nevada

The southernmost known location of whitebark pine within California is found around the Coyote Peaks of Sequoia National Park and Sequoia National Forest. Distribution of whitebark pine continues north in scattered patches on mountaintops. Around the Kings-Kern Divide, whitebark pine occurs continuously across the peaks and ridges of the Sierra crest through Yosemite National Park. The largest stands of whitebark pine in California exist in the southern portion of the Sierra Nevada, where average elevation is much higher than in other parts of the state. Whitebark pine is estimated to be present on 266,400 acres. This acreage spans elevations ranging from 7,150 to 13,500 feet, with an average elevation of 10,430 feet.

From the high country of Yosemite National Park and Humboldt-Toiyabe National Forest, whitebark pine extends northward to Freel Peak with patchy occurrences north and west of Lake Tahoe, becoming more disjunct to the north and at lower elevations. In the northern portion of the Sierra Nevada, whitebark pine is presumed to be present on approximately 47,000 acres across an elevation range of 7,200 to 11,400 feet, with an average elevation of 9,500 feet.

Northern Sierra Nevada vegetation patterns

In Northern Sierra forests, whitebark pine is often found with lodgepole pine, mountain hemlock, red fir, and western white pine. It occasionally co-occurs with Jeffrey pine (*P. jeffreyi*), Sierra juniper (*Juniperus grandis*), and quaking aspen (*Populus tremuloides*). Common shrubs include sagebrush (*Artemisia tridentata*), ocean spray, wax currant (*Ribes cereum*) and mountain currant (*Ribes montigenum*), mountain snowberry, low sagebrush (*Artemisia arbuscula*), and interior goldenbush (*Ericameria linearifolia*). Herbaceous species include native grasses such as subalpine fescue (*Festuca viridula*), squirreltail grass (*Elymus elymoides*), and Bolander's bluegrass (*Poa bolanderi*), which intermix with common perennial forbs like woolly mule's ears (*Wyethia mollis*), mountain monardella (*Monardella odoratissima*), spreading phlox (*Phlox diffusa*), and white stemmed lupine (*Lupinus albicaulis*).

Southern Sierra Nevada vegetation patterns

In the Southern Sierra forests, whitebark pine commonly co-occurs with other pines and conifers such as lodgepole pine, mountain hemlock, and foxtail pine, and occasionally with Jeffrey pine, limber pine, western white pine, or Sierra juniper. In wetter areas, whitebark grows alongside broadleaf trees such as quaking aspen. Shrub cover is variable, but commonly found species include granite prickly phlox (*Linanthus pungens*), Brewer's mountain heather (*Phyllodoce breweri*), ocean spray, wax currant, dwarf bilberry, shrubby willows (*Salix* spp.), shrubby cinquefoil, and Sierra chinquapin. Commonly found herbaceous species such as frosted buckwheat (*Eriogonum incanum*), rosy everlasting (*Antennaria rosea*), Sierra penstemon (*Penstemon heterodoxus*), and mountain pride (*P. newberryi*), are often intermixed with perennial graminoids like shorthair sedge (*Carex filifolia*), Parry's rush (*Juncus parryi*), western needlegrass (*Achnatherum occidentale*), and squirreltail grass.

Krummholz whitebark pine stand on ridge south of Depressed Lake, John Muir Wilderness. Photo by the California Native Plant Society.

Threats

Mountain Pine Beetles

The native mountain pine beetle (*Dendroctonus ponderosae*) has co-evolved with western pine for millennia. Infestations generally fluctuate through forests with mortality events followed by cleansing fire regime events. Mountain pine beetles are considered an important agent of disturbance in maintaining structural and compositional diversity of conifer forests (Weed et al. 2015). More recently, mass beetle infestations have been correlated with increased climatic warming (Mock et al. 2007). A warming climate is particularly impactful in the drier regions of the state, where whitebark pine often grow near lodgepole pine (Cluck 2010). Mountain pine beetles require sufficient thermal input to complete their life cycle in one season. Historically, high elevation ecosystems have not met these needs. However, due to recent warming trends, conditions are frequently adequate at high elevations to complete the beetle's life cycle, and infestations in whitebark pine are becoming increasingly common (Logan and Powell 2001). The preponderance of mass infestations at high elevations has been witnessed throughout California, especially in the arid Warner Mountains and Eastern Sierra Nevada. Data show that the mountain pine beetles have impacted fewer whitebark pines in the Sierra-Cascades and the Klamath-Cascades (14% and 29% respectively) than in the Modoc and Sierra Nevada (60% or greater).

White Pine Blister Rust

In addition to native insects, a non-native fungal pathogen is affecting high-elevation forests. In 1910, white pine blister rust (*Cronartium ribicola*) arrived in a British Columbia port and by 1930 had spread to southern Oregon, infecting western white pine and sugar pine along the way (Murray 2005). White pine blister rust infection (and mortality from blister rust) is more prevalent in the cooler and wetter mountains of the Klamaths and the Cascades; it decreases in prevalence moving southward as the landscape becomes drier. Within the Sierra Nevada-Cascade Region, 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 fewer 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 southern part of California and the Sierra Nevada's relatively hot and dry climate.

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. Dolanc et al. (2013) have presented evidence that warming temperatures may increase recruitment and promote survival of small trees, leading to a 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 mountain pine beetle and white pine blister rust spread (Weed et al. 2013). Thus, rising temperatures may facilitate an expansion of both blister rust and beetles to higher elevations, creating concern for the long-term outlook of whitebark pine (Slaton et al. 2019b). Fires in whitebark pine stands are also increasing in intensity and severity due to warming and drying of the high-elevation landscapes across California. We are only beginning to see and understand the impacts of this phenomenon.

Management Considerations

Managers face multiple challenges related to conservation of the white pine group (e.g., whitebark pine, Western white pine (*Pinus monticola*), sugar pine (*P. lambertiana*), limber pine (*P. flexilis*), and other pines not native to California), including climate change, degradation of white pine ecosystems, and conflicts between restoration activities and wilderness policy. While recognizing the broad suite of threats to whitebark pine, conservation and restoration plans will need to acknowledge the complex dynamics among National Forests, National Parks, and Wilderness Areas throughout California.

Local conservation strategies have the best chance of stemming the loss of key individuals and populations that may be integral to conservation efforts at the range-wide scale. Local strategies may include: seed collection from trees identified as rust resistant, for propagation (Sniezko et al. 2011) and for out-planting (Sniezko and Kegley 2012); treating stands with Verbenone to deter mountain pine beetle attack, especially for cone bearing, blister rust-resistant individuals (Bentz et al. 2005;

Kegley and Gibson 2004); prescribed fire or thinning to reduce interspecific competition (Keene et al. 2012); and identifying and targeting areas that may support future whitebark pine colonizations as the climate continues to change (Shanahan et al. 2016; Chang et al. 2014). This work is ongoing.

Michael Kauffmann is a kindergarten-through-college educator in Humboldt County. He has served as an ecologist with the CNPS Vegetation Program, mapping rare conifers, including whitebark pine. He is the author of Conifer Country*,* Conifers of the Pacific Slope*, and* Field Guide to Manzanitas*. His next book,* The Klamath Mountains: A Natural History *is due in 2022.*
All images are by the author unless otherwise noted.

This article was adapted from Conservation Assessment for Pinus albicaulis *(Whitebark Pine) on National Forest Lands in California with Management Considerations (M. Kauffmann, K.G. Sikes, J. Buck-Diaz, J. Jackson, R. Floreani-Buzbee, and J. Evens), California Native Plant Society Vegetation Program, 2019, revised 2021. Full information for the references in the text can be found there. The document can be accessed online at bit.ly/36ckqln.*

The Pines of California's Channel Islands *by Liz Bittner*

Marisol Villarreal

A canyon on the trail to Pelican Bay on Santa Cruz Island, showing healthy bishop pines with associated vegetation on slopes and near ridge tops.

On the trail to Pelican Bay on Santa Cruz Island in late September, I walk past summer-dormant sagebrushes and needlegrasses, sallow manzanitas, dark green toyons, and bright green lemonadeberry. I also walk past healthy and vigorous bishop pine seedlings of varying ages and sizes emerging from beneath the downed limbs of dead pines. It is refreshing to see these pines doing well and harboring understory plants during the driest time of the year.

Between 13,000 and 8,000 years ago, when California's climate was cooler and wetter, pines and other conifers were much more abundant

Small bishop pines.

Stephen Bednar

One-year-old bishop pines at the Santa Rosa Island restoration site.

on California's Channel Islands. Today California's climate is warmer and drier, and there are just two relict pine species remaining on the two largest islands. Bishop pine (*Pinus muricata*) can be found on Santa Rosa Island as well as Santa Cruz Island, and the Santa Rosa Island Torrey pine (*Pinus torreyana* subsp. *insularis*) exists only in one grove on Santa Rosa Island. Both of these pines were among the first plants to be collected and grown at the Regional Parks Botanic Garden and can still be found in the Channel Island section—as well as beyond the Garden's fence line! One bishop pine, collected from Fry's Harbor on Santa Cruz Island in 1940, remains front and center, and while it was looking questionable last year, it has regained vitality and looks great this year. Santa Rosa Island Torrey pine was collected in 1938, 1975, and 2015. A number of trees from the 1938 collection stand tall both inside and outside the Garden, with new seedlings from the 2015 collection planted among them.

The Garden's trees have lived a protected and pampered life, but life on the Channel Islands was not always this easy for these pines. From the mid-nineteenth century to the late-twentieth century, sheep and cattle ranching took a toll on many plant species on the islands, including these pines. With grazing animals now absent from the islands, many plants are making a healthy comeback. Bishop pine seedlings are doing well and supporting understory plants such as bush monkeyflowers, island buckwheats, and scrub oaks. And the small Torrey pine grove on Santa Rosa Island appears to be expanding. But there are some remaining challenges to the health of these pines on the islands. Some areas of Santa Rosa Island that once supported cloud forests of bishop pine and island oak are now extremely eroded due to the legacy of grazing and are inhospitable to plant life. Due to the fact that the Santa Rosa Island Torrey pine, the rarest pine in North America, is limited to one wild population on Santa Rosa Island and has a very small gene pool, there is some concern about that pine's long term ability to adapt to climate change as well as to pest and disease pressures. The good news is that efforts are underway to face these challenges.

As mentioned above, bishop pine has made a comeback on its own in many places after grazing pressure was removed. However in some locations, such as Soledad Ridge on Santa Rosa Island, the soil was so extremely denuded by grazing animals that plants have not been able to reestablish. Without the presence of plants, rain and heavy winds continue to cause erosion. Soledad Ridge was once home to a cloud forest that captured fog as precipitation, providing water to tree roots as well as to an understory of grasses, shrubs, and subshrubs. In an effort led by Kathryn McEachern of the United States Geological Survey, the USGS, the Channel Islands National Park (NPS), and teams of volunteers have been working to restore the cloud forest. Much of the work took place between 2014 and 2017, with over 7,000 volunteer hours and about 400 individuals helping out! Among other projects, they have constructed devices that capture fog along the ridge to aid in the establishment of pine and oak seedlings and have laid wattles and zig-zag fences across gullies to help hold soil as well as detritus that will help build the soil and reduce erosion. In essence, the work that has been done is meant to jump start the natural processes. Several hundred bishop pines that have been planted on the ridge are thriving, and over time, as the trees become established, they in turn will capture fog on their needles, water the thin soil beneath, and create a hospitable environment for additional tree seedlings and understory plants. The cloud forest will become self-sustaining and be able to restore the floristic diversity of Santa Rosa Island and provide additional ecosystem services to other flora and fauna on the island.

Island Torrey pines have not been planted on Soledad Ridge, as they are not known to have grown along the ridge in recent history. They are found at lower elevations at the northeastern end of Bechers Bay. The USGS/NPS team may consider planting them in other foggy zones on the island, but that strategy will require additional study. While the grove does appear to be expanding, a recent conservation gap analysis of US pines published by the Morton Arboretum in Illinois lists *Pinus torreyana* subsp. *insularis* as critically endangered; out of 419 pines it was ranked the eighteenth most vulnerable to pests and diseases—the most vulnerable pine in the Western U.S. It is in fact the rarest pine in North America. Santa Rosa Island Torrey pine has very low genetic variability and a very small, isolated population (approximately 4,000 individuals), and there is some concern about this pine's long-term ability to adapt to climate change pressures. Some researchers are looking into the viability of genetic rescue as a long-term conservation strategy (Hamilton et al, 2017). Genetic rescue is defined as "the recovery in the average fitness of individuals through increased gene flow into small populations, typically following a

Island Torrey pine cones are larger and rounder than mainland Torrey pine cones.

Island Torrey pine recruitment on Santa Rosa Island, slightly west and downslope from the main grove. This photo was taken in 2015, and the pines have grown healthily since!

Check dams and wattles at the restoration site on Santa Rosa Island showing a healthy population of bishop pines. Marisol Villarreal.

fitness reduction due to inbreeding depression" (Allendorf and Liukart, 2007). A second subspecies of Torrey pine (*Pinus torreyana* subsp. *torreyana*) grows in a few small groves on the San Diego coast at Torrey Pines State Natural Reserve. This subspecies also has a very limited distribution and a small number of individuals (approximately 7,000), but it has slightly more genetic variability. Could a genetic cross with the mainland Torrey pine increase the island species' resiliency in the face of climate change, drought, pests, and pathogens?

In 2006, Jill Hamilton and her colleagues initiated an experiment to answer that question. They utilized seeds from an artificial population of Torrey pines composed of equal numbers of specimens of Santa Rosa Island origin and mainland San Diego-area origin that had been planted at the Scripps Institute in La Jolla before 1960. 643 seedlings from the Scripps Institute plantings were genetically (DNA) analyzed, and 120 seedlings of each of three types—"pure" mainland, "pure" island, and first-generation (F1) hybrids between the two—were planted at a site in Montecito. In 2017 the researchers published the results of their study. While the F1 hybrids do appear to have improved fitness in some traits, such as increased height and earlier cone production, a number of questions remain unanswered. Was the improved fitness in the hybrids a genetic or an environmental response? Is there a benefit to the slower growth rates in the two separate populations, allowing more resources to go to below-ground portions of the trees? Will the improved fitness evidenced in the F1 hybrids be maintained in successive hybrid generations

Lauren Smith

Newly planted bishop pine with irrigation and a fog hat.

Bishop pine seedlings along trail to Pelican Bay on Santa Cruz Island.

or backcrossed individuals? And are there reproductive barriers between the mainland and island populations that have not yet been revealed through this study? Researchers continue to look into these questions, and more, to determine whether genetic rescue is a viable option and how to capture the greatest number of genetic traits in a seed collection.

The two pine species growing on the California Channel Islands are important to the islands' ecosystems, building soil through leaf drop and erosion control, capturing and condensing fog, providing nesting and other habitat for animals both while alive and as downed wood, and more. It is wonderful to see government agencies and researchers alike working toward long-term restoration and conservation of these species.

***Liz Bittner** is the Botanic Garden Supervisor. Along with her management duties, she provides day-to-day care for the Channel Island section of the Garden.*

All images are by the author unless otherwise noted.

REFERENCES:

Hamilton, Jill A., et al. 2017. Genetic Conservation and Management of the California Endemic, Torrey Pine (*Pinus torreyana* Parry): Implications of Genetic Rescue in a Genetically Depauperate Species, *Ecology and Evolution*. 7(18):7370-7381.

Allendorf, Fred W., and Gordon Luikart. 2006. *Conservation and the Genetics of Populations*. Blackwell Publishers.

K. McEachern

Wattles prevent erosion and support plant growth at the Santa Rosa Island restoration site.

K. McEachern

Close up of zig-zag fence to retain detritus and to help build the soil..

Introduction to the Conifers at the Regional Parks Botanic Garden

by Glenn Keator

New cones as well as the previous year's open cones appear on this mountain hemlock (*Tsuga mertensiana*).

California is home to over 50 species of conifers, and we are very fortunate to have an excellent cross-section of them at the Garden. Here is an overview of our collection.

The pine family, Pinaceae, is the major family in California (though recent taxonomic changes suggest that the Cupressaceae may be larger). The pine family has five genera, all of which are represented in the Garden. It is typified by monoecious trees (pollen and seed cones on the same plant) and needle-like leaves. The seed cones vary from tiny and papery to substantial and woody, their scales spirally arranged and bearing two seeds per scale.

The genera fall out like this: *Pinus*, the pines, is the largest group, with many subgroups in the state. Pines bear a fixed number of needles on tiny spur shoots, and their cones are usually woody.

Notable pines in our collection include beach and lodgepole pines, the coastal and mountain varieties of the same species, *P. contorta*; pinyon pine with its edible seeds; gray and Torrey pines with long, grayish needles; Coulter pine with its massive, heavy cones; and bishop and knobcone pines with closed cones that only open after a fire. Mention must also be made of a third closed-cone pine, *P. radiata*, the familiar Monterey pine, which, because of its rapid growth, has been the world's most planted pine for wood products. It is not grown in the Garden, though there are many examples of it growing in Tilden Park.

Perhaps the most famous of all of California's pines is the Great Basin bristlecone pine, *P. longaeva*, considered among the world's longest-lived trees at close to 5,000 years. Ours are small specimens because they grow so slowly.

Our second genus is *Abies*, the true firs, have single needles and upright cones that shatter and fall to pieces when ripe. California has few firs, the most noteworthy being the endemic Santa Lucia or bristlecone fir, *Abies bracteat*a. Restricted to the Santa Lucia Mountains south of Monterey, it may be the rarest fir in the world. Our specimens demonstrate how beautifully these trees can be used in a garden.

The spruces, *Picea* spp., are noted for their scaly bark and hanging seed cones with fluted, papery scales. Our most unique species is *P. breweriana*, the weeping spruce, restricted to the Siskiyou region and very slow-growing.

The hemlocks, *Tsuga* spp., have drooping tips and side branches. While the western hemlock, *T. heterophylla*, has minute, light-weight cones, the mountain hemlock, *T. mertensiana*, is unusual in having more substantial cones like spruces. Our specimens are very slow growing and so have not yet produced cones.

Finally, the Douglas-firs, misnamed because they are not true firs, belong to *Pseudotsuga*, with *P. menziesii*, the common species, widely used for plywood and other applications. Its seed cones hang and fall intact, each rounded scale with a 3-pronged bract draped over it (colloquially referred to as a "mouse tail").

The second major family, in California and in the Garden, is the cypress family, Cupressaceae, which can be tricky to identify. The classical, original family has scale-like leaves, not needles (except in young saplings), but unfortunately (in my opinion) the redwoods have been added, complicating the definition of the family.

The main family consists of four genera with flattened, fern-like branches, and two genera with the more familiar three-dimensional branch patterns. Unfortunately, the four with fern-like branches are incorrectly called cedars (true cedars are in the pine family, have needles, and live in the Old World). Of these false cedars, the incense-cedar, *Calocedrus decurrens*, is by far the most common, a component of mixed-conifer forests in the mountains, with bright yellow-green foliage and strange cones that resemble birds in flight. The

The sprays of incense-cedar (*Calocedrus decurrens*), are made up of elongated scales which extend downward along the stem.

others include the western red-cedar, *Thuja plicata*; the Port Orford cedar, *Chamaecyparis lawsoniana*; and the Alaska yellow-cedar, *Callitropsis nootkatensis*.

The other genera, those without fern-like branches, are *Hesperocyparis*, the western cypresses with woody seed cones that shed seeds only after fire; and *Juniperus*, junipers, with fleshy, berry-like seed cones. While the famous Monterey cypress is missing in our Garden, many other species are present, with our Santa Cruz western cypress, *H. abramsiana*, famous for its great size.

The strangest of the western cypresses is the so-called pygmy western cypress, *H. pygmaea*. Although stunted in many of its coastal habitats, on good soils it attains great size, like the specimen we have.

The junipers include one ground-cover species along with several large shrubs and small trees. While the amazing *J. grandis*, Sierra juniper, attains great size and shape in its homeland, our specimen fails to convey that grandeur.

The redwood clan, although derived from an ancient common ancestor with the rest of the cypress family, is distinctive enough that until recently it was placed in the family Taxodiaceae. Redwoods differ in many respects from the other cypresses, including having needles and pitch-free bark. The coast redwood, *Sequoia sempervirens*, is famous as the world's tallest tree; and the giant sequoia, *Sequoiadendron giganteum*, has the distinction of being the world's most massive tree species. We have beautiful groves of good-sized redwoods and giant sequoias in the Garden, though as redwoods can live 2,000 years and giant sequoias 3,000 years, our specimens are just youngsters.

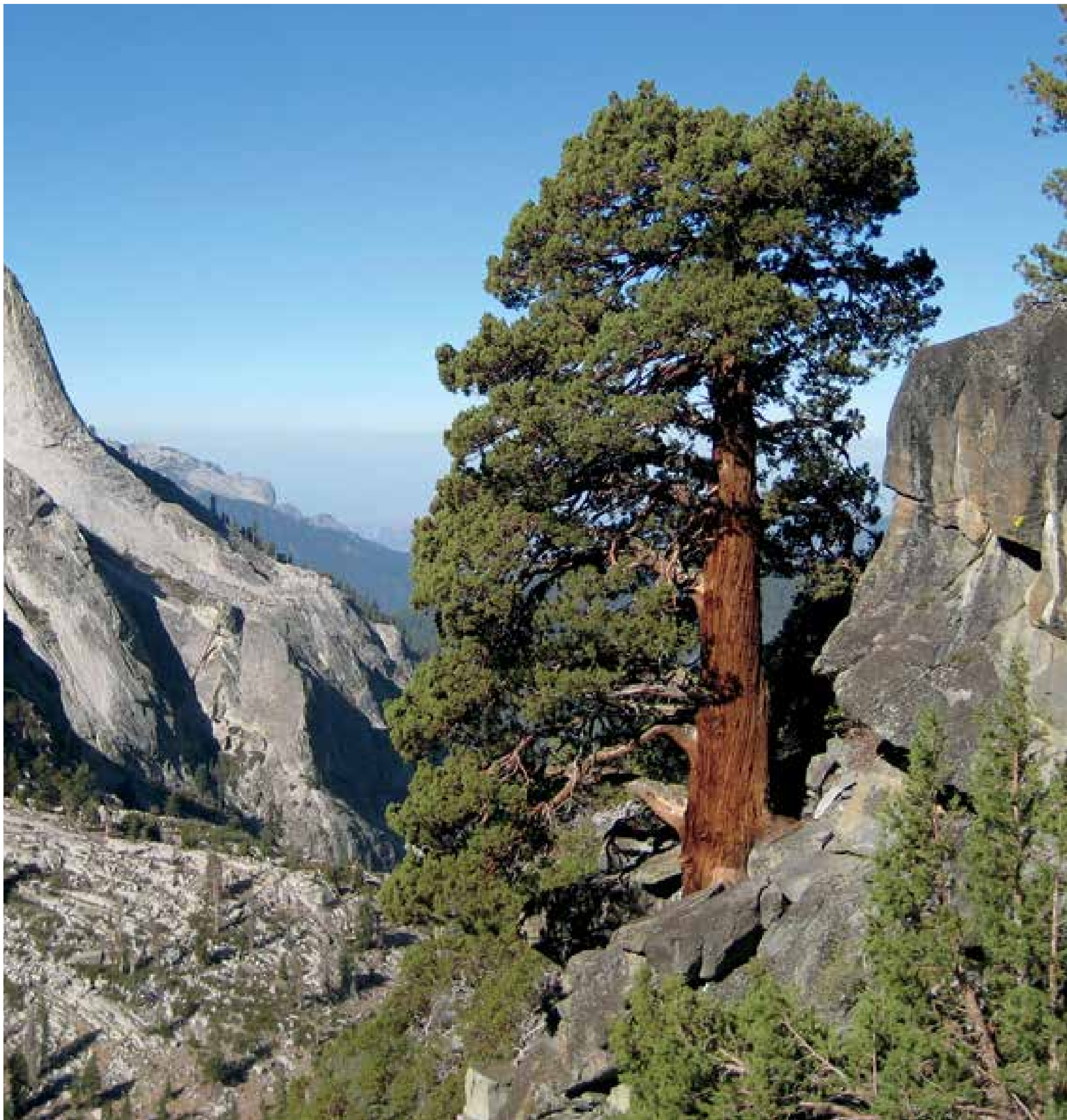
That leaves us with the yew family, Taxaceae, with only two species in California—western yew, *Taxus brevifolia*, and California nutmeg, *Torreya californica*. Both species grow in the Garden. The yew holds its seed in a red, cup-like aril, while the nutmeg, distinctive for its extremely sharp needles, has a green-purple aril around a nutmeg-shaped seed.

Certainly more than one visit is needed to do justice to the Garden's many beautiful conifers.

Glenn Keator has taught many classes at the Regional Parks Botanic Garden and is the author of several books on California native plants.

Photos by Emerald Canary.

Sierra juniper (*Juniperus grandis*) near Hamilton Lakes in Sequoia National Park.



One of the most distinctive features of the Regional Parks Botanic Garden is the "wall of conifers" that towers above all the other trees in the Garden and provides a dramatic separation of the shaded northern part of the Garden from the sunny southern and eastern parts. While our collection of California gymnosperms is nearly complete, the "conifer wall" is composed of relatively few taxa: *Sequoia*, *Sequoiadendron*, *Thuja*, *Chamaecyparis*, one *Hesperocyparis* (*pygmaea*), one *Juniperus* (*grandis*), one *Pinus* (*ponderosa*), and three *Abies* (*concolor*, *grandis*, and *bracteata*). What hides behind the conifer wall? Even more conifers—and the rich assemblage of forest understory plants of the Redwood, Sierran, and Pacific Rain Forest sections of the Garden. Significant but (in this view) hidden conifer components of the "wall" are *Torreya*, one *Pinus* (*contorta* var. *contorta*), one *Picea* (*sitchensis*), and one *Tsuga* (*heterophylla*).

This somber and almost solid backdrop contrasts brilliantly with the myriad green tones of the rest of the Garden. Was that a deliberate plan of James Roof's, or delightful serendipity? We'll likely never know for sure. What we do know for sure is that Roof loved California's conifers and wanted to grow all of them in the Botanic Garden.

California's Gymnosperms: Conifers by Another Name *by Bart O'Brien*

All conifers are gymnosperms, but not all gymnosperms are conifers. However, all gymnosperms native to California are conifers. (Cycads and ginkgos, both commonly found in California gardens, are also gymnosperms, but they are not conifers.) Gymnosperms (literal translation: naked seeds) are an ancient lineage of vascular plants that date to about 390 million years ago, predating the angiosperms (flowering plants) by about 255 million years. Just because gymnosperms are an old lineage does not mean that they have stopped evolving. There are many examples of relatively recent speciation events in our native pines, with the most recent, the divergence of foothill pine (*Pinus sabiniana*) from Torrey pine (*Pinus torreyana*), thought to have happened between five and ten million years ago in the late Miocene.

Gymnosperms produce seeds that are not enclosed by a plant ovary or fruit (this is why they are considered "naked"). The unfertilized seeds are exposed directly to the air and are fertilized after the pollen contacts the pollendrop (a tiny drop of liquid exudate from the tip of an unfertilized seed). All conifers produce seeds in cones that are usually composed of woody scales (though some have fleshy arils instead). The scales vary from extremely thick and woody (like those of most pines—*Pinus* spp.) to intermediate thickness (like those of most firs—*Abies* spp.) to almost papery (as in spruces—*Picea* spp.), and the seeds only become fully exposed when mature. The scales of conifer cones are arranged in spirals along a central axis in what often results in a Fibonacci sequence (the shell of a chambered nautilus is an example of a Fibonacci sequence). There are separate

male and female cones, and in most conifers (but not all), both types are found on the same plant (such plants are called monoecious). Typically the female cones are produced high up in the crown of the plant, and the flimsy, always-ephemeral male or pollen cones are found at the tips of the lower reaches of the plant. This is why you almost never see developing female fir cones or pine cones anywhere near the ground.

Three of California's five juniper (*Juniperus*) species (*californica*, *communis*, and *grandis*) and all seven of our Mormon tea (*Ephedra*) species are typically included with the single-sexed (dioecious) conifers, where female and male cones are on separate plants. However, there are either known or suspected exceptions in all California species in these two genera.

Interestingly, two of California's native gymnosperms produce single seeds that are surrounded by fleshy arils rather than woody or papery cones. These are California nutmeg (*Torreya californica*) and Pacific yew (*Taxus brevifolia*), and they are solely dioecious. Female plants of California nutmeg have a green- to purplish aril that completely covers the seed and is firmly attached to the seed coat. Female plants of Pacific yew typically have a red (sometimes green) aril that is always open at the top and is never attached to the seed coat. Why are such fleshy-seeded plants considered conifers, since there are no female cones? The answer is not all that obvious—it is because of their ephemeral male cones.

Bart O'Brien is the Director of the Regional Parks Botanic Garden.

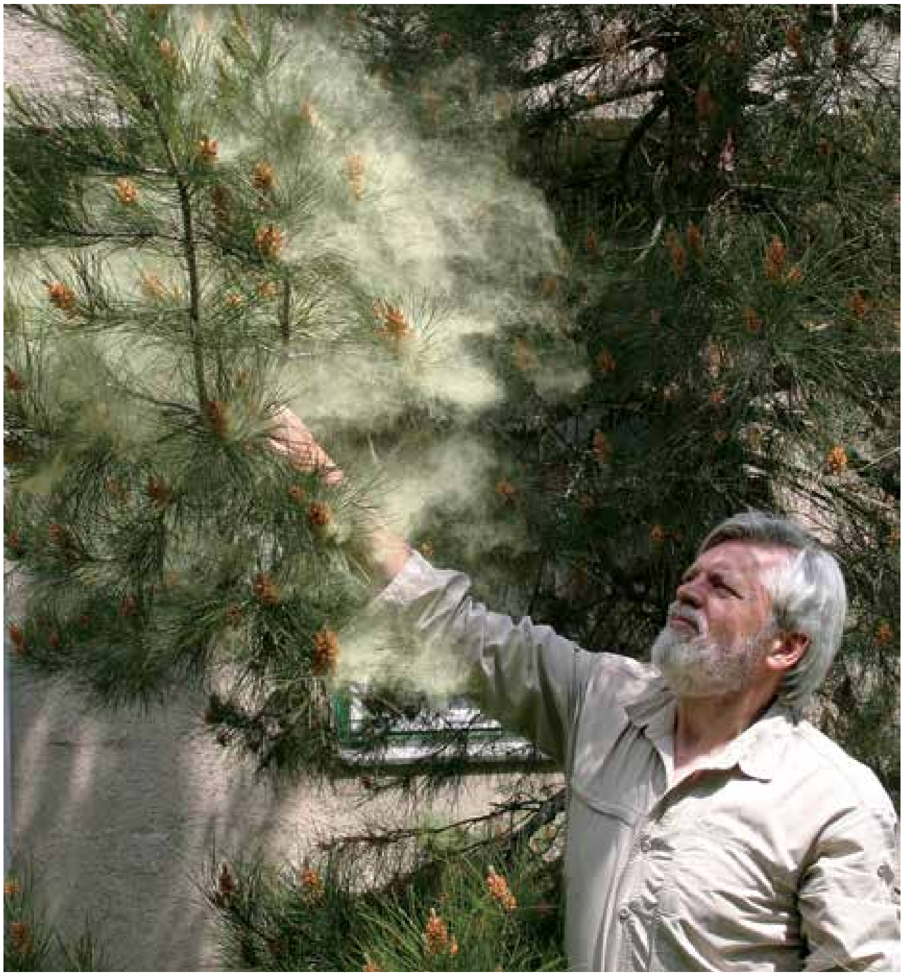
Photo by the author.

California and California Floristic Province conifers present in the Regional Parks Botanic Garden as of Septemer 30, 2021. There are 66 taxa present, and one additional seed collection.

Abies amabilis
Abies bracteata
Abies concolor
Abies grandis
Abies lasiocarpa
Abies lasiocarpa var. *lasiocarpa*
Abies magnifica
Abies magnifica var. *magnifica*
Abies magnifica var. *shastensis*
Abies procera
Callitropsis nootkatensis
  (*Chamaecyparis nootkatensis*)
Calocedrus decurrens
Chamaecyparis lawsoniana
Ephedra californica
Ephedra viridis
Hesperocyparis abramsiana var. *abramsiana*
  (*Cupressus abramsiana*)
  ours is the largest known specimen
Hesperocyparis forbesii
  (*Cupressus forbesii*)
Hesperocyparis goveniana
  (*Cupressus goveniana*)
Hesperocyparis guadalupensis CFP BAJA
  (*Cupressus guadalupensis*)
Hesperocyparis macnabiana
  (*Cupressus macnabiana*)
Hesperocyparis montana CFP BAJA
  (*Cupressus montana*)
Hesperocyparis nevadensis
  (*Cupressus arizonica* subsp. *nevadensis*)
Hesperocyparis pygmaea
  (*Cupressus pygmaea*)
Hesperocyparis sargentii
  (*Cupressus sargentii*)
  (*Cupressus sargentii* var. *duttonii*)
Hesperocyparis stephensonii
  (*Cupressus arizonica* subsp. *arizonica*)
  (*Cupressus stephensonii*)
Juniperus californica
Juniperus communis var. *depressa*
Juniperus communis var. *jackii*
  (*Juniperus communis* var. *saxatilis* 'Jackii')
Juniperus communis var. *saxatilis*
  (*Juniperus communis* var. *sibirica*)
Juniperus grandis
  (*Juniperus occidentalis* var. *australis*)
Juniperus occidentalis
  (*Juniperus occidentalis* var. *occidentalis*)
Juniperus osteosperma SEED ONLY
Picea breweriana
Picea engelmannii
Picea sitchensis
Pinus albicaulis
Pinus attenuata
Pinus balfouriana subsp. *austrina*
Pinus balfouriana subsp. *balfouriana*
Pinus contorta subsp. *bolanderi*
Pinus contorta subsp. *contorta*
Pinus contorta subsp. *murrayana*
  (*Pinus murrayana*)
Pinus coulteri
Pinus edulis
Pinus flexilis
Pinus jeffreyi
Pinus lambertiana
Pinus longaeva
Pinus monophylla
  (*Pinus californiarum*)
Pinus monticola
Pinus muricata
Pinus ponderosa var. *pacifica*
Pinus ponderosa var. *washoensis*
  (*Pinus washoensis*)
Pinus quadrifolia
Pinus radiata var. *radiata* *OUTSIDE FENCE*
Pinus remorata NOT IN JEPSON
  (*Pinus muricata*)
Pinus sabiniana
Pinus torreyana subsp. *insularis*
Pseudotsuga macrocarpa
Pseudotsuga menziesii var. *menziesii*
Sequoia sempervirens
Sequoiadendron giganteum
Taxus brevifolia
Thuja plicata
Torreya californica
Tsuga heterophylla
Tsuga mertensiana

Pollen and Pollination Drop: California's Conifers "In Bloom"

by Zsolt Debreczy



The author with an Eldar pine (*Pinus brutia* var. *eldarica*) at time of pollen release. Pollen cones, the male complement of the more iconic female cones, are often found on the lower part of conifer trees.

OVERVIEW

Pollen

I remember the first time I saw a thick layer of yellow pollen on our windowsill in Boston in the spring of 1988. Having lived in European broad-leaved forest zones until then, I hadn't seen "clouds" of conifer pollen before. The black pines, Scotch pines, Colorado and Norway spruces, eastern red cedars, Oriental arborvitae, some cypresses and cedars, and the local yew that were scattered throughout the yards and hillsides of my hometown all released their pollens almost unnoticeably, just like the wind-pollinated hazels and oaks in the nearby forest. But in the Boston area and in almost all of New England, the former broad-leaved forests were cut down soon after colonization; and one-and-a-half to two centuries later, in the "post-agriculture era," the former agricultural lands were colonized by pines, mostly eastern white pines (*Pinus strobus*). Typically a pioneering tree in the line of vegetation succession, it creates favorable conditions for resettlement by hardwood or mixed hardwood-coniferous forests until eventually a flora- and climate-balanced climax forest community is realized. And white pines release a prodigious amount of pollen.

How much pollen? Wind-pollinated plants do release an astronomical number of pollen grains. In conifers, the loblolly pine (*Pinus taeda*) may serve as an example. Loblolly has been much studied because of its importance for forestry in the southeastern US. The *USDA Pollen Management Handbook*, 1981, counted some 3,500–4,000 grains of pollen produced in each pollen cone. The tip of a branchlet of Loblolly pine generally develops a "cluster" of some 25–30 pollen cones. Consequently, a single, ultimate branchlet may produce some 100,000 pollen grains. A mature tree has 150–200 pollen cone-bearing, ultimate branch systems each with about 50 clusters of pollen cones; one tree has the potential to release some nine billion pollen grains, and a loblolly plantation of just 1,000 mature trees could release as many as nine trillion.

How far can pollen travel? Loblolly pine pollen has been known to travel south of its original source some 3,000 km, using the north-south prevailing wind patterns. In comparison, data confirming the 260-km journey of conifer pollens from Hungary to Cracow, Poland, seem barely worth a mention.

Wind pollination vs. insect pollination

87% of the world's 352,000 terrestrial green plants are animal/insect pollinated. 78% of the green plants in the temperate zones are animal/insect pollinated, and 94% of those in the tropics. Thus, 22% of plants in the temperate zones are wind pollinated, in contrast to just 6% of plants in the tropics. Gymnosperms (the "naked seed" plants, the majority of which are conifers) play a rather negligable role in these figures. The 1,050 gymnosperms represent just 0.3% of the world's plants and would represent 1.4% of the anemophilous (wind-pollinated) ones if all gymnosperms were anemophilous; however, they are not.

Aerial pollen transmission evolved much earlier than animal pollination. Gymnosperms are an ancient group, with maidenhair trees (Ginkgoales) going back to the Permian period (~300 to 250 MYA) and modern conifers (Coniferales) back to the Triassic (~250 to 200 MYA). As far as we know today, wind pollination was the only widely successful pollen transmission strategy during the early evolutionary history of seed plants. Conifers, the dominant forest component of the late Paleozoic and Mesozoic eras, were wind pollinated hundreds of millions of years before the first evidence of the presence of pollinating insects. In fact, the appearance of the primary pollinating insects such as Hymenoptera (bees, wasps, ants, etc.) and Lepidoptera (butterflies and moths) in the late Mesozoic (~250 MYA) and through the Tertiary and Quaternary (from ~66 MYA to the present) coincides with the unfolding of the flowering plants, the angiosperms. The conifers that make up the main component of the temperate-zone forests (predominantly the Holarctic zones north of Mexico and Africa, but to a lesser degree the Holantarctic of southern Chile, Argentina, and New Zealand) were evolved for wind pollination and remain wind pollinated. In North America the 13 most common genera of the temperate zone forests are exclusively wind pollinated, with two further genera having both entomophilous and anemophilous species. In contrast to these 13+2 genera, the 24 broadleaf-tree genera within the same zones are animal pollinated.

Rather surprisingly, several of the most ancient gymnosperms, which are in fact the true tropical ones, are insect pollinated, though through much of their geologic history there were no pollinating insects! For example, the purely tropical genus *Gnetum* has interesting bisexual fertile shoots and releases pollination drops that have a sweet scent and attract insects. Some Mormon teas (*Ephedra*), as well as *Welwitschia*, also produce pollination drops, and insects play a role in their pollination. Ancient groups such as cycads in the wider sense (Cycadaceae, Strangeriaceae, Zamiaceae)—today with ~300 extant species, some of which have been traced back over 200 million years—are insect pollinated, even though, at the time of

The reproductive main stem of the tropical gymnosperm gnetum (*Gnetum gnemon*) with pollination drops and pollen. Members of the *Gnetum* genus are thought to be some of the first plants to have evolved insect pollination.

Female reproductive structure of Chinese ephedra (*Ephedra sinica*) with pollenation drops.

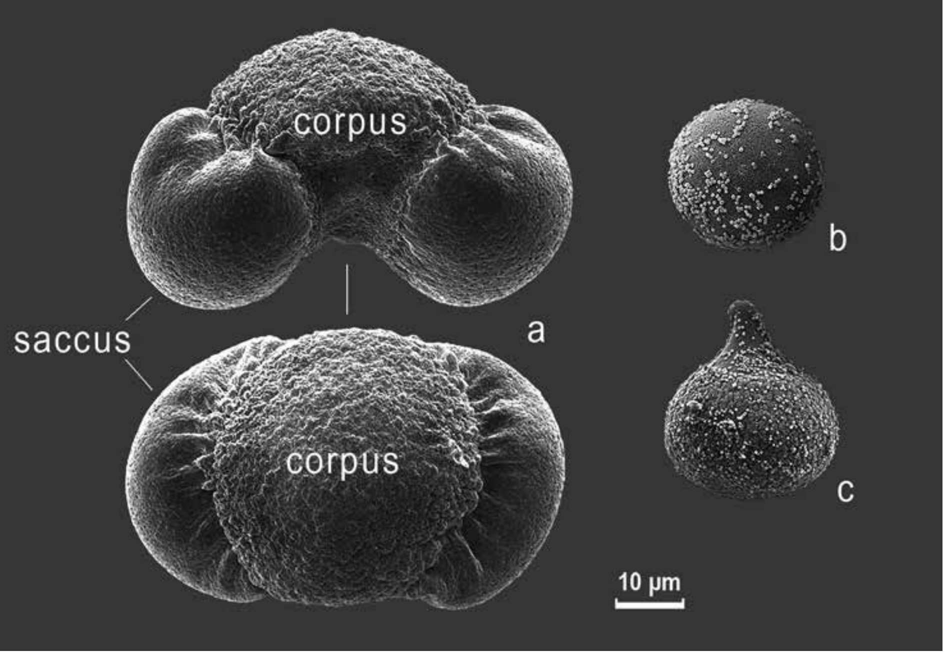
Kevin C. Nixon

their main era of flourishing, pollen-consuming insects were not yet known to exist. The first evidence of the presence of pollinating insects is proved by a pollen-covered thrips fossil found in northern Spain in early Cretaceous deposits that have been dated at 110 to 105 MYA.

Animal pollination is particularly interesting if one considers that when Earth's angiosperm forests evolved, beginning in the early Cretaceous Period (145 to 100.5 MYA), the climate was much warmer than it is today. The average global temperature was over 20 C, as compared to 14 C today and 12 C during the ice ages. In tropical climates today, wind accounts for just a small percent of pollination.

Gymnosperms and Angiosperms

Besides different transportation systems in their stems and the gymnosperms' lack of a double fertilization, the main difference between gymnosperms and angiosperms is in the development and function of their carpellary structure, the sperm-to-egg delivery system. In angiosperms, this is the *ovary-style-stigma complex*. In gymnosperms this set of structures does not exist; instead, the ovule develops on an open carpellary leaf or seed scale of a cone or a cone-like structure. This open, modified-leaf-like structure with uncovered ovules is the source of the word "gymnosperm," meaning "naked seed" or "revealed seed" in Greek. However, the term is not entirely correct. After pollination



A composite of scanning electron microscope images of bisaccate versus non-saccate conifer pollen grains. a) Pondersosa pine (*Pinus ponderosa*) bisaccate pollen, front and back views, b) Greek juniper (*Juniperus excelsa*) non-saccate pollen grain, and c) giant sequoia (*Sequoiadendron giganteum*) non-saccate pollen grain. The saccus is the wing-like bladder that helps keep the pollen grain airborne and the corpus is the main body of the pollen grain. Sacci are present in some genera, such as *Pinus*, *Abies*, and *Picea*, and not present in others, such as *Pseudotsuga*, *Tsuga*, *Thuja*, *Juniperus*, *Sequoia*, and *Sequoiadendron*.

Pollen images from Palynological Database (PalDat.org); photographs by J. Halbritter and J. Bouchal.

on open seed scales, with few exceptions (like yews, for example), the seeds do become fully covered soon after fertilization. The seed scales and seeds in the pine and cypress families are hidden between tightly overlapping cone scales and bracts. In some members of the yew family, like California nutmeg and its Asian relatives, the seeds are completely enveloped by structures called arils that are composed of a fleshy scale or scales. Several genera of the mainly subtropical-tropical family of podocarps (Podocarpaceae) have completely covered seeds; soon after fertilization the seed scales, equipped with vascular tissue up to the ovule, will envelop the developing seeds.

Pollination

Pollination is the transfer of pollen from the male reproductive organ to the corresponding female organ in seed plants. Now the question is how the pollination of angiosperms differs from that of gymnosperms. In angiosperms (the flowering plants), pollens are often sticky or barbed for better attachment to a pollinator's skin or coat, while in the majority of gymnosperms, which are wind pollinated, the pollens are smooth and often equipped with sacs (sacci) or a bladder that help keep them aloft in the air. In angiosperms the pollens are captured by a rounded, lobed, or feathery stigma where the pollen germination and pollen-tube development take place. But how does the "cellular courtship" happen? How does the stigma determine if the pollens that arrived are the right ones to support germination? Pollen grains of angiosperms interact with stigma through a wide range of information in which the two structures mutually "determine" whether there's a match. These interactions have been thoroughly studied by a range of sciences from biochemistry to physics, but there is still much we need to understand, for example how the stigma and pollen molecules regulate self-recognition, the workings of the self-incompatibility response to avoid interbreeding, and the stigmatic enzymes that provide pollen tube guidance.

Considering the complicated nature of stigma-pollen studies, it may appear that fertilization is easier for gymnosperms, where the ovules are open, simply sitting uncovered on the carpel ready to be fertilized. Yet compared with the easily visible size of an angiosperm stigma, the gymnosperm's micropyle (the opening through which the pollen enters the ovule) is tiny, and it doesn't take many pollen grains to block it. Further, many of them might be the pollen of other species; or of the same individual, which would result inbreeding. Nature, of course, has a "strategy" against these eventualities: the pollination drop.

The Pollination Drop

Thorough research has helped classify how gymnosperm pollens get attached to the nucellus (where the seed will mature) and the egg cell in the ovuliferous scale complex. The nucellus exudes a sugary and/or scented fluid, the

Sergii Dymchenko

Bisaccate pollen grain of an unspecified conifer as seen magnified 100 times, stained with iodine, with a horizontal field of view of about 0.17 millimeters.

"pollendrop," or more correctly, the "pollination drop." This discovery goes back to 1959 but only received proper attention some 40 years later.

The pollination drop has two main functions: capturing aerially borne pollen grains or attracting pollinator insects. Plus, there is a related function, the so-called "post pollination drop," which in some genera (Douglas-fir in California) has the role of protecting the ovule from infection by fungi and bacteria.

Pollination drops assist with pollenation by increasing the area of the receptive surface of the ovule. Saccate pollen is restricted mainly to the pine family (with the exception of Douglas-fir and hemlock in California, and beyond these, the genus *Larix*, elsewhere). This pollen floats on air-filled bladders or sacci, and entry into the micropyle is dependent on the gradual constriction (reabsorption) of the pollination drop. The shrinking of the drop draws pollen into the ovule, where it germinates. In the case of the non-saccate pollens of cypresses, yews, giant sequoia, and redwood in California, the pollens expand when wetted in the pollination drop and are carried into the micropyle as the drop contracts. In pines the pollen-tube growth is arrested in the nucellus of the ovary, and the zygote will be formed only in the next growing season. Another interesting characteristic related to ancient gymnosperms such as cycadophytes and ginkgo is that their male cells are motile. The pollen grains (having developed on separate male trees of the species) reach the pollendrop on the cones of the female trees and develop motile, flagellate spermatozoids.

The pollination drop contributes to the selection of "same species" pollen as well as enhancing self-incompatibility to avoid self-pollination. Constituents of the ovular secretions are widespread among extant gymnosperms including conifers, cycads, and jointfirs and their relatives (gnetophytes). Pollendrops have been observed in all families (but not all genera) of conifers except monkey puzzle tree relatives, the araucarias. In Douglas-fir, and hemlock in the California flora, no pollendrop develops; instead, male nuclei reach ovules with the development of pollen tubes. In the northern hemisphere, so far only firs and some hemlocks have been found not to produce ovular secretions (Douglas-firs have hidden, "post-pollination, pre-fertilization" drops). There is also a correlation between pollination drops and insect pollinators. For example insect-pollinated jointfirs have been found to have much greater sugar content than any wind-pollinated conifer.

FAMILIES AND GENERA

EPHEDRACEAE, the Jointfir Family

Ephedra **(Jointfir, Jointpine, or Mormon Tea)**

Mainly insect pollinated via pollination drop, typically dioecious.

Jointfirs are "primitive" gymnosperms sometimes considered part of the Gnetaceae family, a tropical, broad-leaved gymnosperm group. *Ephedra* is the only extant genus in the Ephedraceae family. Worldwide total of 69 species (though sometimes given as 40). Both wind and insects play a role in their pollination. There are 12 species native to North America and eight to ten taxa to South America, the rest to Europe, North Africa, central Asia and dry parts of southeast Asia. Small trees or shrubs; some are climbers or dwarf shrubs. Almost all species have seeds enveloped by fleshy red, yellowish, or white arils. American taxa and the one Asian taxon have paper-thin sterile and fertile bract scales surrounding the ovule's outer layer and the seeds.

PINACEAE, the Pine Family

Approximately 252 species with 11 genera all native to the Northern Hemisphere (a single pine, *Pinus merkusii*, extends south of the Equator). Six genera in the western US, four in Europe, three in North Africa, and eight across eastern Asia (though cedars exist only in the Mediterranean Basin and western Himalayas). All members of the pine family are monoecious (female seed cones and male pollen cones develop on the same tree). Seed cones typically appear on the upper, stronger branches in firs and in the Asian genus cork-fir (*Keteleeria*) as well. Less typically, cedars, spruces and white pines tend to develop cones in the upper part of the crown. In the rest of the Pinaceae genera worldwide, cones appear all over the crown (on the West Coast such is the case in *Larix* and *Tsuga*). Pollen cones in all genera develop on any type of weaker, lower branches as well. All pine relatives have two seeds (rarely only one) that develop on their ovuliferous fertile scales in the axils of the so-called "fertile bracts."

Pinaceae genera of the world: *Abies*, *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pinus*, *Pseudolarix*, *Pseudotsuga*, *Tsuga*.

A single female cone of Santa Lucia fir (*Abies bracteata*) with its characteristic very long, thin resin-tipped bracts.

Abies (the Firs)

Pollen saccate, no pollination drop; monecious.

67 species, 20 varieties worldwide (though the numbers are often given as 52 species, one subspecies, 12 varieties). Eight are native to the West Coast of the US. One of the main characteristics of firs is that their cones disintegrate when fully mature, leaving only the naked cone axes on the branches (the axis is either thick or thin, a character typical for each taxa). Female cones are always upright. Seed scales may be longer than the bracts, hiding the bracts; or the bracts may extend beyond the seed scale. Among the Western firs, five have hidden bracts (Pacific white, grand, red, Pacific silver, and subalpine) and three have exserted (or protruding) bracts (noble, Shasta red, and Santa Lucia). Among these, three species have extra characteristics that are unique in the world: Noble fir has the largest and widest cones of all firs, >22 x 10 cm, (but not the longest!). Unique is the fact that these huge cones are often fully covered with pointy, heart-shaped, broad-winged bract scales. The cones of Shasta red fir are quite similar to noble fir cones at first sight; however their exserted bracts hide the cone scales much less. The third unique West Coast species is Santa Lucia fir, restricted to a small portion of the Central California coast. The bracts are very thin and much longer than cone scales, reaching up to 5 cm, each with a pearl of resin at its end.

Picea (the Spruces)

Pollen saccate, pollination drop, monoecious.

34 species and 20 varieties worldwide (often given as 35–40 species). Most taxa are native to southeast Asia. In number of species per land area, Japan is the richest, with six distinct species in an area somewhat smaller than California. Only one species occurs in eastern North America and three almost all across the whole Canadian life zone. Three taxa are native to California.The Engelmann spruce, a Rocky Mountain native, is a real relict in northern California, with a few locations only; the other two species are confined to the West Coast. The Sitka spruce ranges from Alaska to northern California, with several specimens exceeding 96 m in height with trunk size <4.4 m in DBH (diameter at breast height). The other Pacific taxon is the Brewer spruce of Northern California and adjacent Oregon. It has the most spectacular crown of all spruces, with elegantly arching main side branches and up to 2.5 m-long, drooping branches and branchlets. Spruces (except a single taxon in the Caucasus) have upright ovuliferous cones at the time of pollination. The outspreading ovuliferous scales form small umbrellas that catch upward-floating pollen, and the bracts are hidden (note that the visible scales of the cone-inflorescences are bracts in firs vs. ovuliferous scales in spruces). After pollination the young cones turn downward and the ovuliferous scales press close like a raincover to protect the developing seeds. The pollen cones, up to three cm long and typically purplish or pink, usually develop close to the apices of the one-year-old branchlets in the spring.

Ovuliferous cones of yezo spruce (*Picea jezoensis*), a spruce native to the Far East, at time of pollination. The fertile scales on these two- to three-inch-long cones are outspreading and form small umbrellas to effectively catch upward floating pollen grains. After fertilization the young cones turn downward while the scales become appressed to protect the developing seeds.

Pinus (the Pines)

Pollen saccate, (hidden) pollination drop, trees monecious.

128 *Pinus* species worldwide. The American continents are the richest in pines, with 77–80 known Mexican species, 15 species native to eastern North America, and 21 on the West Coast. As with firs, the world's most unique *Pinus* species

are in California. Coulter pine has the heaviest cone in the hemisphere and the second longest (after sugar pine). Mature Coulter pine cones, on a short stalk (a "peduncle"), can be 45 cm long and weigh 5 kg when fresh. The cones of sugar pines are up to 60 cm long on a stalk up to 16 cm long, yet weigh barely 2 kg when wet.

Pine-cone inflorescences are upright, formed by short bract scales arranged singly or in whorls of up to six in some species, such as knobcone pine (*P. attenuata*). After pollination, no fertilization occurs; instead the pollen nuclei remain in the micropyle area and only fertilize the egg cell in the next season, at which point the conelet starts to develop to full size. When mature, pine cones may hang down or remain erect. They may fall to the ground after maturity or (as in most American pines) remain closed on the branches, with seeds viable for decades; this strategy, called serotiny, waits on fire to open the cones. Finally, the cones of a few pines disintegrate on the tree instead of falling.

Pseudotsuga (the American Douglas-firs)

Pollen saccate, post-pollination/pre-fertilization drop, monecious.

Douglas-fir (two species) has a huge range in the US, from the Rockies to the west coast and south to Oaxaca, Mexico (and a species in Eastern Asia as far east as Japan). The West Coast Douglas-fir (*P. menziesii* var. *menziesii*) is known to be the tallest conifer ever recorded on Earth (119.78 m before it fell in 1930), and a tree exists today that is known to have reached 13.32 m (43.7 feet) in circumference. Douglas-firs' ovuliferous cone inflorescences are more or less upright at first, and the fertile scales are completely hidden by the mostly three-pointed bracts. After fertilization the cones rapidly bend downward and the bracts are partly hidden by the growing cone scales. The male pollen cones are arranged around the axils of the one-year-old branchlets, somewhat like in firs, unfolding with papery, thin bud- and bract scales. Before the pollen sacs split, the axes of the male cones extend, making the pollen cones even more loosely pendulous.

Tsuga (the Hemlocks)

Pollen saccate, no pollination drop, monecious.

Nine species and three varieties, evenly distributed between eastern Asia and North America and almost so in eastern and western North America. Canadian and Carolina hemlocks grow in the east, Pacific and mountain hemlocks in the west. Hemlocks have mostly short, flat needles, though they vary in length depending on their positions within the spiral order on the branch. The cones are small and typically green before fully maturing, with papery-thin cone scales. The only exception is the mountain hemlock of the eastern US, found particularly on the higher slopes, with short, fleshy needles that are roundish in cross section and cones up to eight cm long (the longest of all the hemlocks), often purplish before maturing. Both ovuliferous and pollen-cone inflorescences appear on short side branchlets from terminal buds or occasionally on branchlet apices. Cones mature in one season.

Coulter pine (*Pinus coulteri*) pollen cones shedding pollen.

Upright green ovuliferus cone and downward-facing pollen cones of Douglas-fir (*Pseudotsuga menziesii*).

CUPRESSACEAE, the Cypress Family

Some 150 species in 30–32 genera, with eight genera on the American west coast. Most cypress family members have globose to oval cones, small and woody (true cypresses) or leathery or fleshy as in junipers. Most conifers have winged seeds, but in the cypress family all but one species have small wingless or marginally winged seeds. The exception is incense cedar, with elongated cones and long-winged seeds. The ovuliferous cone-inflorescences are very small and scarcely noticeable in all species. Male cones typically have 8 to 10 pairs of scales. In cypresses, pollination happens in mid- to late autumn; however, the cones only start to develop in the spring. Some of these fully develop in one year; others, like true cpresses, Nootka cypress, and some junipers, need two years to mature, thus they have a "conelet phase." Number of seeds/cones in the cypress family varies from four (incense cedar) to several hundred (giant sequoia, redwood, and true- or western-cypresses).

Calocedrus (the Incense Cedars)

Pollen non-saccate, pollination drop, monoecious.
Only three taxa belong to this genus, one in California and two in Asia (including a variety in Taiwan). All are restricted to the Northern Hemisphere. Unlike other Cupressaceae in America, *Calocedrus* has alternating long and short leaf scales developing in whorls of four and cones with two fully developed seed scales. In contrast to other American Cupressaceae, *Calocedrus* seeds have long wings that develop in pairs on each fertile seedscale. Pollination/fertilization happens typically in mid autumn, but the small conelets do not continue to develop until mild weather early in the spring.

Macnab cypress (*Hesperocyparis macnabiana*) with pollen cones.

Cupressus and *Hesperocyparis* (the Cypresses)

Pollen non-saccate, pollen bursts in pollination drop, monoecious.
23 species, mainly in Mediterranean climates, but also occur in monsoon subtropical and summer-rain tropical climates and in desert environments as well. 15 species in North America, of which four taxa are restricted to Mexico and Central America; five species occur in Asia. The most diverse genus is in America, where recently the cypresses were separated from the Eurasian taxa as *Hesperocyparis*. The vegetative part of *Cupressus* is in general very similar to scale-junipers, but their needle-like juvenile leaves are soft (not sharp). Cones can be large (1–4 cm) and woody, with scales often warty from resin blisters. Each cone scale hides a large number of seeds, for several hundred per cone (vs. 1–2 up to 13 seeds in junipers). Cones develop in two years (the first year the conelets are smaller and not fully woody). Cones can be serotinous and persistent on branches. Typically release pollens in autumn, some early in the spring. The best-known *Cupressus* is the tall and narrow Italian cypress; California's famous Monterey cypress, with its umbrella-shaped crown, is now in the genus *Hesperocyparis*.

Interestingly, true cypress is the only gymnosperm known to have asexual reproduction (called apomixes or agamospermy in plants): in the rare Sahara cypress (*Cupressus dupreziana*), the seeds develop entirely from the genetic content of the pollen.

Juniperus (the Junipers)

Pollen non-saccate, pollen bursts in pollination drop, dioecious.
Junipers are widely distributed in the Northern Hemisphere and some of them reach the tropics, with a single species in Africa. Ranging from massive trees to shrubs and creeping varieties, and may be found on seashore sand, rocks, or in high elevations. Some junipers, including California's common juniper (*Juniperus communis*), have sharp, needle-like leaves, with leaves and cone scales arranged in whorls of three. *J. communis* is California's only needle-species. Mature trees of the three other California species develop decussate, scale-like leaves, closely pressed to the stem. Cones are typically rather small, oval to ovate or globose; most of them are blue when mature, although in some species pruinose white, or pinkish, or pruinose red.

Sequoiadendron (Giant Sequoia)

Pollen non-saccate, pollen bursts in pollination drop, monoecious.
Formerly classified in the family Taxodiaceae, the giant sequoia is the most massive organism on Earth. In 1975 most of the Taxodiaceae genera, including giant sequoia, were reclassified to be included in the cypress family (Cupressaceae). In giant sequoia the leaves are in spiral order on main shoots, and they are sharp pointed, but they are smaller and blunt pointed on side branch systems. The seed-cone inflorescences develop terminally, mostly on the ends of arching, stronger,

Zoya Akulova

Immature seed cones of western red cedar (*Thuja plicata*) begin to develop during mid-summer.

main branches. They are narrow, 1.2–1.5 cm long, 0.4 cm wide, and consist of purplish green, fine-pointed fertile bracts with ovuliferous scales at the base. The pollen cones are 4–8 mm, developing terminally on short axillary side branches anywhere in the crown. Seed cones develop to half or two-thirds of full size and remain green in the first year, then finally mature to brown in the subsequent year.

Sequoia sempervirens (Redwood)

Pollen non-saccate, pollen bursts in pollination drop, monoecious.

Monotypic genus with a single species. Currently the tallest tree in the world (a Douglas-fir was the tallest [119.78m] until it fell in 1930). Redwoods typically pollinate in spring, with both ovuliferous and pollen cones on tips of the one-year-old branchlets. Cones are terminal on short scaly shoots, small (1.5–3.5cm), and many-seeded. They mature in one year.

Thuja plicata (Western red cedar)

Pollen non-saccate, pollination-drop, monoecious.

Five species (two in China, one in Japan, and two in North America). Western red cedar is the largest member of the genus, reaching 75 m in height with a trunk up to 6.23 m in DBH; it is thus one of the tallest and most massive of the conifers. Lower branches often curve down and have adventitious roots, so that a single tree may form a small "forest of the giants." The leaves are compressed tightly to the branches in a folded pattern (*plicata* means plaited or folded), with upper sides bright green and lower sides grayish. The female conelets are scarcely visible (three mm in receptive phase), with tiny pollination drops. The pollen cones are five to eight mm and reddish to purplish before fully mature. The cones are small (0.4–1.4 cm), and rather thin scaled, maturing pruinose-green to yellowish-green and finally to brown, and releasing two to three seeds/scales, with marginal wings.

TAXACEAE, the Yew Family

Pollen non-saccate, pollen bursts in pollination drop, dioecious (except Canadian yew, which is monoecious).

There are some nine yew species in the world, four of them in North America. Yews are not conifers in the narrow sense, having no cones but instead a single shoot, each with a single seed. The seed is partially covered by sterile bract scales and in most species is surrounded by a fleshy aril that is open at the top, at first leathery green, later juicy and red. However, in some yew family members, like *Torreya* (California nutmeg), the seeds are completely enveloped by the aril-type structures. Except for *T. canadensis*, all taxa are typically dioecious (pollen cones and seed-shoots develop on separate plants).

Torreya (California nutmeg)

Pollen non-saccate, pollination drop, dioecious.

The genus is known from America (two species) and Southeast Asia (four species). Needles are leathery, stiff, in some species sharply pointed. The cone-inflorescences develop in short axillary shoots; the pollen cones unfold in the spring with sterile bracts, while the ovuliferous cones unfold with two fertile scale-pairs. Only one of the two ovules pollinates, developing first into a small, conical-ovoid conelet that stays dormant until the next spring, at which time the seed and aril fully mature. California nutmeg's seed (<4.2 cm) and aril complex may reach 5 cm in length. The typically ovoid aril completely covers the seed.

California nutmeg (*Torreya californica*) pollen cones during pollen release.

Zsolt Debreczy *lives in Budapest, where he is the research director of the International Dendrological Foundation (NDA Inc.). He is the co-author, with István Rácz, of* **Conifers Around the World** *(two volumes).*

All photos are by Zsolt Debreczy and István Rácz unless noted.

FURTHER READING

Tomlinson, P.B. 1994. Functional morphology of saccate pollen in conifers with special reference to Podocarpaceae. International Journal of Plant Sciences vol. 155, No. 6, pp. 699-715. University of Chicago Press.

Ting, William S. 1965. The Saccate Pollen Grains of Pinaceae Mainly of California. Grana. Vol. 6, No. 2, pp. 270-289, https://www.tandfonline.com/doi/abs/10.1080/00173136509429148.

Pilgrim in Coniferland *by Emerald Canary*

Editors' Note: For the last 14 years, Emerald Canary has been the designer of *Manzanita*. With the publication of this issue, she retires from the magazine to which she has made such a huge contribution. Thank you, Emerald! We wish you Happy Trails and many more years of successful conifer hunting.

The coolest cone ever is not a cone! California groundcone (*Kopsiopsis strobilacea* formerly *Boschniakia strobilacea*), is a member of the broom-rape family that parasitizes nearby roots. Because it's a parasite, it does not photosynthesize and thus does not have green leaves. But it does have flowers, little ones that are shown above.

How It Began

I was an art student finishing up undergraduate studies at UC Santa Barbara, and an elective course in botany and plant ecology sounded like a wonderful idea, especially the field trips all across California. The course opened up new vistas for me, and about the same time I took a marvelous course in the English Department called something like Nature Writing. Aside from multiple papers to write and classes to attend, the real substance of the course was backpacking trips in the Sierra; I think the first was in early April! I always found something to write about.

At the time, the late sixties to early seventies, there was a new openness in my world, and I was highly receptive. It was a time to expand horizons and challenge conventions. Even the word ecology was new and cosmic. Botany was an exciting discovery to explore alongside my direction as an art student. I marveled at the diverse ways in which plants adapted to the environment.

From the mid-seventies to the mid-nineties I lived in Colorado and spent much of my time hiking and climbing in the Rocky Mountains and taking pictures of trees. This became my obsession, nurtured by my earlier courses in botany. For a while I had a darkroom, and I exhibited black and white photos of trees at local libraries. It was always trees; I have rarely photographed people.

Back in California in the 2000s, botany courses and field trips with Glenn Keator and Stew Winchester taught me to pay close attention to trees, and photography was a good way to pay attention. Chemical photography evolved into digital photography. My love of high-altitude conifers crystallized, and those tough survivors were the first objects of my fascination. Somewhat later Michael Kauffmann's books, *Conifer Country* and *Conifers of the Pacific Slope*, plus a field seminar with Michael in the Russian Wilderness, were extremely helpful in locating populations of rare conifers.

Ultimately my love of conifers morphed into a website, **www.coniferous.site,** in which I explore native and exotic conifers and other gymnosperms.

In this article I describe four of my favorite conifers: Alaska-cedar, Brewer spruce, foxtail pine, and Pacific silver fir. Brewer spruce grows only in a few isolated spots in the Klamath Mountains of northwest California and southwest Oregon. Alaska-cedar and Pacific silver fir both reach their southernmost limits in the Klamath Mountains; foxtail pine grows here also, and more extensively 300 miles away in the southern Sierra. Due to geology, topography, and climate, the multiple ranges of the Klamath Mountains contain associations of conifers that occur nowhere else in the world.

The Future

When I write "find," I mean identify, correctly, myself, not just accept the word of whatever expert is nearby. One of the trees I have so far failed to find on my own in California, where it sneaks into the Klamath Mountains, is subalpine fir (*Abies lasiocarpa*), a constant timberline companion in the mountains of Colorado. I actually saw some in the Russian Wilderness but could not find an angle where I could photograph the extremely narrow spire diagnostic of this tree.

I will find subalpine fir in 2022!!

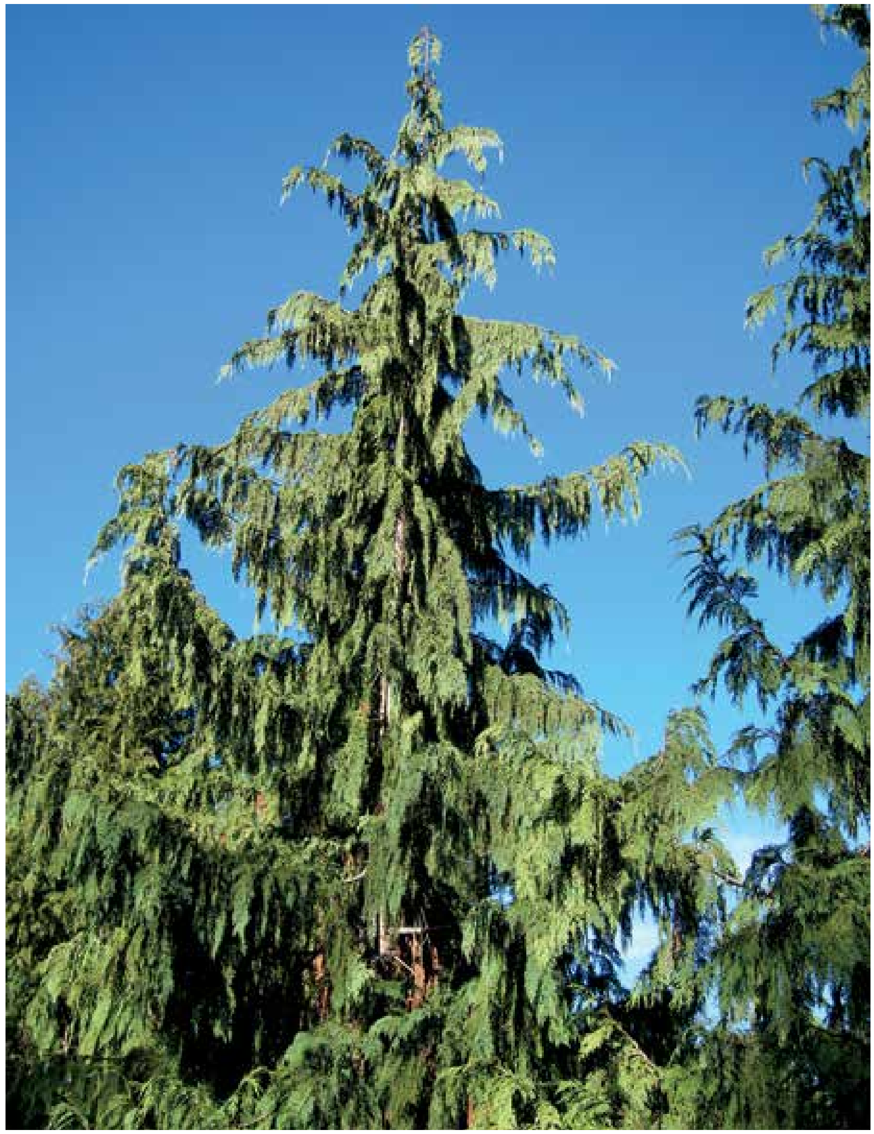
Emerald Canary after a wrong turn on the way to Man Eaten Lake in the Marble Mountain Wilderness.

Alaska-Cedar (*Callitropsis nootkatensis*)

Alaska-cedar, also called yellow-cedar (of which the disputed genus has been variously *Chamaecyparis*, *Cupressus*, and *Xanthocyparis*), extends from coastal mountains in Alaska south to a very few locations in the Siskiyou Mountains in Northern California at 4,500 to 6,900 feet. It can grow to 130 feet in the northern part of its range, but in the Siskiyou Wilderness, at the extreme southern range of the species, the trees I saw were not half that tall. My first encounter with Alaska-cedar was at Buck Lake, and later I found more at nearby Devil's Punchbowl, both in Six Rivers National Forest in the Siskiyou Wilderness.

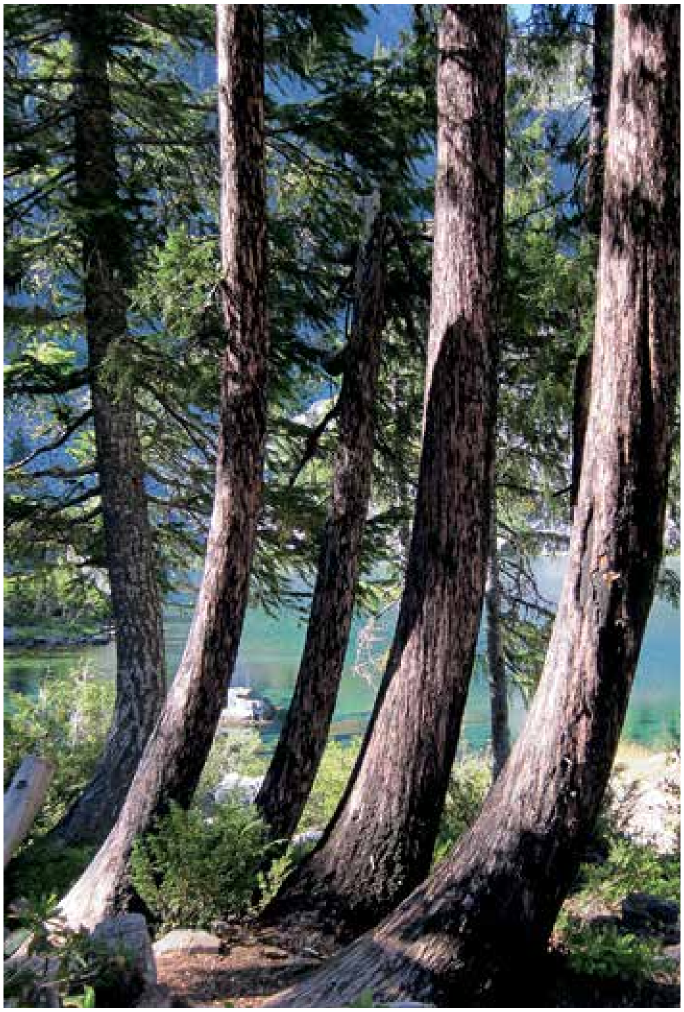
Alaska-cedar thrives in coastal rainforests, often growing with Pacific silver fir and mountain hemlock. Its vertical, hanging foliage sheds snow. Recent research into large-scale die-offs indicates that Alaska-cedar depends on heavy coastal snowpack for insulation. Thinner snowpacks due to climate change have allowed increased damage from freezing.

Alaska-cedar can live over a thousand years. Specimens 1,636 and 1,834 years old have been found from ring counts of stumps in clear-cuts in British Columbia (Earle, **http://www.conifers.org/**). It has been considered one of the finest timber trees in the world and is used by many Northwest Coast peoples for bows, paddles, dishes, and many other items.



My photos of Alaska-cedar from Buck Lake and Devil's Punchbowl were not outstanding, but fortunately the Garden has two superior examples of this species. One is pictured here.

Scale-like needles are small. Seed cones are spherical, take two years to mature, and have spikes or horns at the end of each scale, like a large juniper "berry" with spikes. They are about one-third inch in diameter.



These Alaska-cedars comprise a small stand at Devil's Punchbowl, at 4,840 feet in Six Rivers National Forest. In the photo you can see one stump at the lower left side. I have learned that more than a dozen of these trees were cut between 2009 and 2012—for what? For firewood?! Michael Kauffmann has written an excellent blog post about this incident: https://www.michaelkauffmann.net/2014/07/the-cry-of-the-wilderness-and-c-nootkatensis/

Brewer Spruce (*Picea breweriana*)

I discovered Brewer spruce in 2014 on a field seminar with Michael Kauffmann in the Russian Wilderness of the Klamath Mountains. Brewer spruce has an unforgettable silhouette, with long, dark, pendulous branches. It is found only in the Klamath Mountains in northwestern California and southwestern Oregon. I sought them out again and again.

Brewer spruce is nowhere abundant, but in its limited range it is not uncommon. It grows in simple or diverse conifer forests and may occur with western white pine, sugar pine, foxtail pine, Shasta red fir, white fir, noble fir, Douglas-fir, incense-cedar, and mountain hemlock. In the Russian Wilderness "Miracle Mile," where an amazing 18 conifer species have been discovered in one square mile, it occurs near Engelmann spruce, which makes a rare appearance here, far from its prime habitat high in the Rocky Mountains.

Brewer spruce occurs in scattered stands on ridges and north- and east-facing slopes at an elevation of 3,000 to 9,000 feet and thrives with annual precipitation of 50 to 100 inches. It is often outcompeted on optimal sites, but it will tolerate deep shade, drought, cold, and a wide range of soils, including

Brewer spruce above Boulder Creek Lakes, Trinity Alps Wilderness. What a gift to find this magnificent specimen near our campsite.

serpentine. Those I've seen have been mostly in full sun. Brewer spruce usually grows to 50 to 75 feet, though is occasionally much larger, and may attain five feet in diameter. Some individuals may live 900 years.

I saw some lovely Brewer spruce at Grizzly Lake in the Trinity Alps in 2021, one so large I thought it might be a champion (but I think they're all champions, so I don't pay much attention to that). Now I regret that I didn't take the time to count them and notice exactly where the much more common Shasta fir (*Abies magnifica* var. *shastensis*) prevailed. Much of that area was burned in the Haypress (River Complex) Fire in the fall of 2021, including the trees where we camped in June. However, the Brewer spruce at Grizzly Lake survived.

Cones dangle from short branchlets and are two to five inches long with thin, rounded, smooth-margined scales.

A remarkable inhabitant of the Russian Wilderness is sugarstick, also called candystick (*Allotropa virgata*), which is incapable of photosynthesis and instead gets its nutrients from fungi associated with tree roots.

Needles occur singly on a woody peg (characteristic of all spruces), and are somewhat prickly, though not nearly as prickly as Engelmann or Sitka spruce needles.

Brewer spruce at Grizzly Lake in the Trinity Alps. Caesar Peak is in the background, krummholz hemlock below.

Foxtail Pine (*Pinus balfouriana*)

Foxtail pines (*Pinus balfouriana* subsp. *austrina*) near Rae Lakes Basin, Sequoia-Kings Canyon Wilderness.

I first saw foxtail pines in Horseshoe Meadow in the Southern Sierra on a field trip in 2003. It was an exciting and beautiful trip in which we explored diverse plant communities, but for me, foxtails were the highlight; I would return many times to learn about and photograph them. I had known about the famous bristlecone pines (*P. longaeva*) of the White and Inyo Mountains but had not heard of their equally spectacular cousins, the foxtails, which inhabit the Sierra roughly 75 miles to the southwest. Foxtail pines are limited to two relatively small areas in California, separated by 300 miles: the Klamath region of northwest California and the southern Sierra, primarily Kings Canyon and Sequoia National Parks. There is speculation that these disjunct populations were contiguous in an extensive subalpine forest 12,000 years ago when there was greater summer rainfall (Johnston 1994).

While these trees were new to me, and because they grew at high elevations in only two locations in California, I considered them to be rare and special. Special they are, but they are common and thriving above 10,000 feet in the Southern Sierra. Over the years, I've felt absolute glee at finding them on many trips into Kings Canyon and Sequoia National Parks, and it is hard to refrain from taking photos of every one. I realized they were not rare, as I'd imagined, but surviving nicely, albeit in a very small niche. They inhabit many locations from 10,000 feet to timberline in Kings Canyon and Sequoia National Parks and from 6,000 to 8,000 feet, usually on serpentine soils, on "sky islands" in the Klamath Mountains.

Foxtail pines are divided into two subspecies: the northern population is *Pinus balfouriana* subsp. *balfouriana*, and the southern population is *P. balfouriana* subsp. *austrina*. Southern Sierra foxtail pine is neither super-cold tolerant nor super-heat/drought tolerant. It occupies an ecological zone between whitebark pine (*P. albicaulis*), which grows between 9,000 and 11,000 feet, and limber pine (*P. flexilis*), which grows between 8,000 and 11,000 feet on dry, windy southern exposures east into the Rocky Mountains. Whitebark pine is able to survive at the very highest altitudes and ridgelines because it protects itself from fierce, cold winds by morphing into a shrubby form known as krummholz. However, foxtails remain erect, though they are often wind-blasted.

Foxtails generally grow in open stands, so fire is a less significant determinant of their survival than climate (although research is needed on fire ecology). However, the National Parks Service prohibits campfires above 10,400 feet in the Sierra in order to protect foxtail pine forests and their remnant downed-wood resource.

Needles are short, occur in bundles of five, and may stay on the branch for many years, thus giving the foxtail appearance.

Cones are three- to five-inches long and have thickened scale tips.

To the left is the narrow form of foxtail pine (*Pinus balfouriana* subsp. *balfouriana*) that grows in the Klamath Mountains.

Foxtail pines in the Klamath Mountains are generally narrower and have darker bark than the southern Sierra foxtail pines. The bark is different enough that a novice botanist might not know they were the same species.

Southern Sierra foxtail pine.

Klamath Mountains foxtail pine.

Pacific silver fir (*Abies amabilis*)

Seeing the large purple cones was thrilling. Unmistakable ID! These trees were on the peninsula next to Hancock Lake where I camped. What a pleasure to see this tree after experiencing the confusing jumble earlier (opposite page).

For the name alone I had to see it. In *Conifer Country*, Michael Kauffmann describes a hike to Hancock Lake in the Marble Mountains, where one can find the southernmost stand of Pacific silver fir. It was the Fourth-of-July weekend, 2015. I had time to do this hike and was curious to see Pacific silver fir, new to me and not correctly identified until the 1930s (Lanner 1999). Spurred by a wonderful description, I set out on the long hike to Hancock Lake. The elevation was low, the grade was gentle, and there was lots of shade. Higher up, English Lakes and Diamond Lake were not inviting places to camp, but the peninsula at Hancock Lake (6,345 feet), with maybe a dozen campsites, was spectacular, and I had the whole peninsula to myself! I was thrilled to find beautiful and identifiable specimens of Pacific silver fir. The Klamath Mountains contain Shasta fir, noble fir, subalpine fir, and white fir as well as Pacific silver fir. Without seeing cones, as Michael writes, firs can be "spectacularly confusing."

Pacific silver fir extends from a very few locations in the Klamath Mountains, around 6,000 to 7,000 feet, north to southeast Alaska, where it grows at sea level. The ones I saw at Hancock Lake were smallish trees; however, outside California they are large forest trees (to 225 feet) and an important timber species. Seed cones are 4 to 6 inches long, purplish, and clustered at top of the tree. Trees can live 300 to 500 years. Pacific silver fir grows in cool, wet

This campsite is unacceptably close to the lake, but all the campsites were like this on the small, narrow peninsula.

conditions on moist north slopes and prefers sites with heavy snowpack. It is shade-tolerant, has thin bark and shallow roots, and is highly susceptible to fire. It may grow alongside Douglas-fir, mountain hemlock, western hemlock, Shasta fir, western white pine, Brewer spruce, and others.

__Emerald Canary__ is an artist and graphic designer.

Photos by the author.

Needles I observed had a soft, fluffy quality, and the undersides have two silvery white stomatal bands.

My first sighting of Pacific silver fir was in this jumbled area near Diamond Lake. As befits my amateur status, scenes like this baffle me. In this photo, Pacific silver fir grows with the more abundant Shasta fir and there are a few mountain hemlocks. Canopy decline is primarily due to fir engraver beetles (*Scolytus ventralis*). This was 2015, in the middle of a multi-year drought, and Diamond Lake was more marsh than lake.

Hancock Lake in the Marble Mountains.

REFERENCES:

BOOKS

Johnston, V. 1994. *California Forests and Woodlands: A Natural History*. University of California Press.

Kauffmann, M. 2012. *Conifer Country*. Backcountry Press.

2013. *Conifers of the Pacific Slope*. Backcountry Press.

Lanner, R. 1999. *Conifers of California*. Cachuma Press.

Sawyer, J. 2006. *Northwest California: A Natural History*. University of California Press.

Turner, M. and E. Kuhlmann. 2014. *Trees and Shrubs of the Pacific Northwest*. Timber Press.

WEBSITES

The Gymnosperm Database, http://www.conifers.org/, Christopher Earle, Editor, is a superb source of scientifically accurate information about conifers and allies. Other useful websites are http://www.calflora.org/, http://www.conifercountry.com/, and https://www.coniferous.site/.

FRIENDS OF THE
REGIONAL PARKS
BOTANIC GARDEN
PO Box 21074
Oakland, CA 94620-1074

REGIONAL PARKS
Foundation
Supporting East Bay Regional Parks

East Bay
Regional Park District

The Garden is open from 8:30 a.m. to 5:00 p.m (5:30 in summer) every day except New Year's Day, Thanksgiving, and Christmas.

The Garden's free e-newsletter, *The Botanic Garden Monthly*, is a terrific source of information about the Garden's plants, features, and natural history as well as special events. To subscribe to the newsletter, and more, visit the Garden's website at **www.nativeplants.org.**

Wayne Roderick Lecture Series

Join us for our popular series of free public lectures on a broad array of topics related to plants and natural history. Named in honor of its founder, the Wayne Roderick Lecture Series takes place on Saturdays at 10:00 AM online through Zoom. These illustrated presentations are enjoyable for beginners and professionals alike. All lectures are free and open to the public.

Saturday, February 26, 2022: Alan Harper on his new bilingual book *A guide to the Flora of the Sierra de San Pedro Martir*
Saturday, March 5, 2022: Joe Dahl, Desert Field Work Over Time
Saturday, March 12, 2022: Chris McCarron, field work and new discoveries in Mount Shasta area
Saturday, March 19, 2022: Michael Uhler, Southern Sierra Alpine Trips
Saturday, March 26, 2022: Liz Bittner, Trips to the Channel Islands

Advance registration is required. Visit **www.nativeplants.org** to sign up.

PLANT SALES CONTINUE AT THE GARDEN!

Looking for some new native plants for your garden? We continue to offer plants for sale, at the Potting Shed below the Anza View Road entrance. For a detailed list of plant availability, go our our website: **www.nativeplants.org.**

Sale hours: Mondays, Wednesdays, and the first Saturday of every month, from 10 a.m. to noon.

Thank You to these Nurseries for Providing a Discount to Members

Annie's Annuals and Perennials (510-215-3301), 740 Market Avenue, Richmond, www.anniesannuals.com
Bay Natives Nursery (415-287-6755), 10 Cargo Way, San Francisco, www.baynatives.com
Berkeley Horticultural Nursery (510-526-4704), 1310 McGee Avenue, Berkeley, www.berkeleyhort.com
California Flora Nursery (707-528-8813), 2990 Somers Street at D Street, Fulton (north of Santa Rosa), www.calfloranursery.com
Central Coast Wilds (831-459-0655), 336 Golf Club Drive, Santa Cruz, www.centralcoastwilds.com (please call before visiting)
East Bay Wilds Native Plant Nursery (510-409-5858), 2777 Foothill Boulevard, Oakland, www.eastbaywilds.com
East Bay Nursery (510-845-6490), 2332 San Pablo Avenue, Berkeley, www.eastbaynursery.com
Flowerland Nursery (510-526-3550), 1330 Solano Avenue, Albany, www.flowerlandshop.com
Larner Seeds (415-868-9407), 235 Grove Road, Bolinas, www.larnerseeds.com
Mostly Natives Nursery (415-663-8835), 54 B Street, Unit D, Point Reyes Station, www.mostlynatives.com
Oaktown Native Plant Nursery (510-387-9744), 702 Channing Way, Berkeley, www.oaktown@oaktownnursery.com