Pinus ponderosa var. washoensis, Washoe pine 2018

Figure 1—Washoe pine on Mt. Rose, Nevada. ©2012 image by Gary A. Monroe, hosted by CalPhotos.

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ABSTRACT

Washoe pine is a variety of ponderosa pine with a limited distribution in eastern California and western Nevada. It grows on all aspects in the upper mixed-conifer and lower subalpine zones. Presettlement stand structure of Washoe pine communities is unknown.

Washoe pine tends to be shorter and have thicker, more glaucous needles than other varieties of ponderosa pine. Washoe pines of all age classes are shade intolerant. Washoe pine maintains dominance on high-elevation, harsh sites with or without fire. On other sites, it generally succeeds to shade-tolerant species such as white fir without fire.

Although little information was available on the fire ecology of Washoe pine in particular, there is a great deal of information on the fire ecology of ponderosa pine at the species level. Ponderosa pine's adaptations to fire include thick bark; a high, open crown; self- and fire-pruned branches; large, scale-protected buds; high foliar moisture content; deep roots; and rapid root growth of seedlings. Crown-stored ponderosa pine seeds generally survive low- and moderate-severity fire but are killed if scorched. Fire resistance of ponderosa pine trees increases with age. Saplings and pole-sized trees generally survive low-severity fire. Mature ponderosa pines generally survive moderate-severity fire as long as the protected bud scales are not scorched. Some large trees survive as much as 100% crown scorch, although ability of Washoe pine to recover after substantial crown kill is undocumented. Crown fires kill ponderosa pines of all age classes.

The fire regime of Washoe pine communities is not well documented. Limited information suggests a historical fire regime of low- to moderate-severity surface fires and mixed-severity fires (with some overstory mortality) at 3- to 40-year intervals.

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INTRODUCTION

FEIS ABBREVIATION
PINPONW

COMMON NAME
Washoe pine
Washoe ponderosa pine

TAXONOMY
The scientific name of Washoe pine is *Pinus ponderosa* var. *washoensis* (H. Mason & Stockw.) J.R. Haller & Vivrette (Pinaceae) [11, 54, 119]. It is in subsection *Ponderosae* of the *Pinus* genus [73].

The taxonomy of ponderosa pine is in flux [41, 125], with the accepted number and nomenclature of ponderosa pine infrataxa in dispute. Varieties of ponderosa pine are distinguished by genetics, morphology, and geographical location [22, 54, 119]. Generally accepted varieties include:

Pinus ponderosa var. *benthamiana* (Hartw.) Vasey, Pacific ponderosa pine
Pinus ponderosa var. *brachyptera* (Engelm.) Lemmon, southwestern ponderosa pine [119]
Pinus ponderosa var. *ponderosa* C. Lawson, Columbia ponderosa pine [11, 54, 119]
Pinus ponderosa var. *scopulorum* Engelm., Rocky Mountain ponderosa pine
Pinus ponderosa var. *washoensis* (H. Mason & Stockw.) J.R. Haller & Vivrette, Washoe pine [11, 54, 119]

Farjon [31] considers Washoe pine synonymous with *Pinus ponderosa* var. *ponderosa*. However, Critchfield [23] noted that in field trials, only about one-third of seeds resulting from a *Pinus ponderosa* var. *ponderosa* x *Pinus ponderosa* var. *washoensis* cross were viable, suggesting genetic distinctions between the two varieties.

Washoe pine is thought to have evolved through hybridization of *Pinus ponderosa* var. *ponderosa* and *Pinus ponderosa* var. *scopulorum*. In modern times, Washoe pine hybridizes occasionally with *Pinus ponderosa* var. *benthamiana* and *Pinus ponderosa* var. *ponderosa* [11, 23, 24, 25, 79, 87]. Different pollination times help prevent hybridization between Washoe pine and these cooccurring varieties of ponderosa pine [23].

Griffin and Critchfield [44] reported that although Washoe pine occurs at about 8,000 feet (2,400 m) in the Warner Mountains—within and above the Jeffrey pine zone—there is a "broad band of intermediates" between the ponderosa, Jeffrey, and Washoe pine zones [44], suggesting hybridization and introgression among the three yellow pines [23]. Seeds of Jeffery pine × Washoe pine crosses have very low viability [23].

Since Washoe pine is a variety of ponderosa pine, characteristics that apply to the species as a whole apply to Washoe pine. Information specific to Washoe pine is reported in this review when it was available in the literature. However, information on the general ecology and fire ecology of Washoe pine was sparse as of 2018, so information is provided at the species level when information on Washoe pine in particular was lacking.

Because *Pinus ponderosa* var. *benthamiana* and *Pinus ponderosa* var. *ponderosa* are not often distinguished in the literature, these varieties are referred to as "ponderosa pine" in this review. See table A1 for a complete list of common and scientific names of plant species discussed in this review and links to FEIS Species Reviews.

SYNONYMS

Pinus ponderosa subsp. *washoensis* (H. Mason & Stockw.) A.E. Murray (cited in [52])
Pinus washoensis H. Mason & Stockw. [37, 55]

LIFE FORM

Tree

DISTRIBUTION AND PLANT COMMUNITIES

GENERAL DISTRIBUTION

Washoe pine has a limited distribution in California and Nevada. It has the smallest distribution of all pines in subsection *Ponderosae* of the *Pinus* genus [73]. Washoe pine is most common on the Modoc National Forest of northeastern California [109], where it occurs in the southern Warner and Bald mountains [24, 44, 55, 69]. Washoe pine is generally rare in Nevada [54]. It was logged extensively in Nevada during silver mining in the late 19th century. As a result, it was nearly extirpated [55]. In northwestern Nevada, it occurs in Galena Creek Canyon above Boomtown and on Mt. Rose [24, 44, 55, 69]. Kartesz [54] extends Washoe pine's distribution into southeastern Oregon.

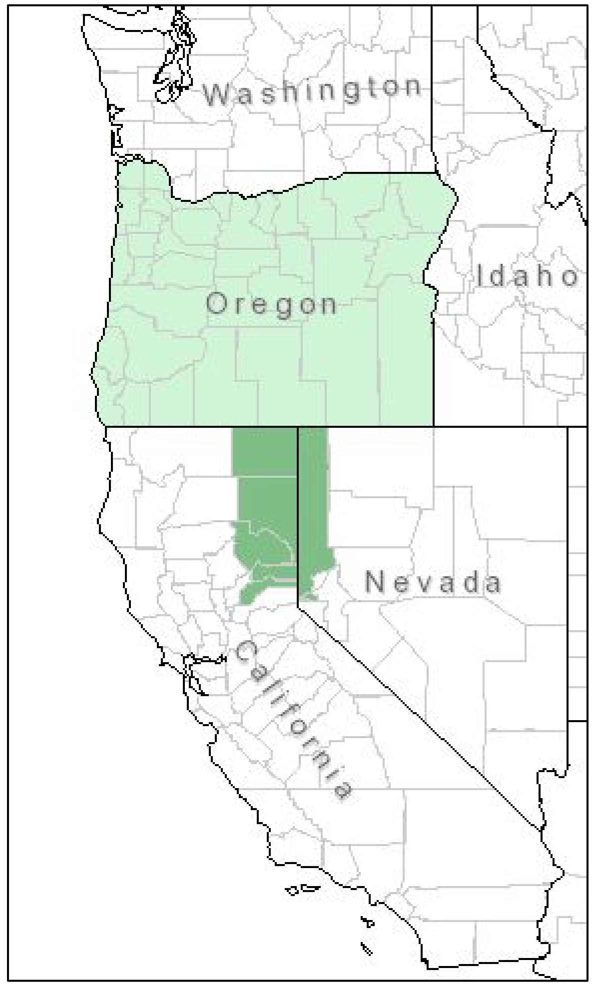

Figure 2—Distribution of Washoe pine. Map courtesy of USDA, NRCS. 2018. The PLANTS Database. National Plant Data Team, Greensboro, NC. [119] [2018, September 10].

States [54, 119]:
CA, NV

SITE CHARACTERISTICS AND PLANT COMMUNITIES

Site Characteristics

The climate zone in which Washoe pine grows is harsher than the lower-elevation zone in which ponderosa pine is common [25, 87, 88], with greater extremes of temperature [87, 109] and less productive soils [90, 109]. Winters are cold, with much of the precipitation falling as snow, and summers are dry [83, 88].

Washoe pine grows in the upper mixed-conifer and lower subalpine zones. It occurs on all aspects, on slopes ranging from 0% to at least 60% [75, 109]. In California, Washoe pine occurs from 6,550 to 9,800 feet (2,000-3,000 m) elevation; rarely, down to 5,000 feet (1,400 m) [11]. It cooccurs with Jeffrey pine from 6,000 to 6,900 feet (1,800-2,100 m) [11]. On the Northeastern Plateau (includes the Modoc Plateau and the extreme northwestern Great Basin), Washoe pine occurs from 6,200 to 8,200 feet (1,890-2,500 m) [37, 88]. In Nevada, it occurs from 6,500 to 8,000 feet (2,000-2,400 m) [44, 55].

Soils are typically coarse to gravelly clays or clay-loams. In the northern portion of Washoe pine's range, parent materials are mostly volcanic, grading to granitic in the southern portion [83, 109]. Jeffrey pine-

Washoe pine communities often occur on ultramafic soils; parent material includes strongly serpentinized peridotite [75]. On Buck Mountain in the Warner Mountains, Washoe pine/pinemat manzanita/Wheeler bluegrass communities occur on soils derived from rhyolite and obsidian. There are no associated tree species [90].

Plant Communities

Washoe pine grows in mixed-conifer and pure stands. In mixed stands, Washoe pine typically grows with Jeffrey pine, white fir, and western white pine [116]. It cooccurs with Jeffery pine throughout most of Washoe pine's distribution [89]. Washoe pine is sparsely distributed in upper-elevation California red fir forests of the southern Cascades and northern Sierra Nevada. Pure Washoe pine stands are generally at higher elevations than mixed-conifer stands [116].

The Washoe pine woodland alliance of California and Nevada occurs from 6,890 to 9,350 feet (2,100-2,850 m) elevation on all aspects. Associated conifers include California red fir, Jeffrey pine, ponderosa pine, Sierra lodgepole pine, western white pine, and white fir [75, 83, 88]. The canopy is open to intermittent; usually, <82 feet (25 m) in height. The shrub layer is sparse and composed of species common to the Great Basin. These may include antelope bitterbrush, curlleaf mountain-mahogany, greenleaf manzanita, mountain big sagebrush, pinemat manzanita, and snowbrush ceanothus. Common herbaceous species include tailcup lupine, tuber startwort, and various graminoids [75, 83].

The Jeffrey pine-Washoe pine woodland alliance occurs on the Modoc Plateau, in the Klamath Mountains, and on the east side of the southern Cascade Range, from 2,000 to 9,500 feet (600-2,900 m) elevation. Slopes are moderate to steep (12%-60%). The alliance is common on all but north-facing aspects. Associated tree species are many, the most common being California red fir, coast Douglas-fir, giant chinquapin, incense-cedar, ponderosa pine, singleleaf pinyon, and western white pine. The canopy is intermittent and usually <82 feet (25 m) in height. The shrub layer is also diverse, although it may be sparse. Antelope bitterbrush, curlleaf mountain-mahogany, dwarf ceanothus, greenleaf manzanita, mountain big sagebrush, pinemat manzanita, and wedgeleaf ceanothus are common. Herbaceous species include Idaho fescue, prairie Junegrass, western needlegrass, common beargrass, tailcup lupine, western yarrow, and woolly mule-ears [75].

In the Warner Mountains, Washoe pine dominates the conifer zone from 6,700 to 7,200 feet (2,040-2,195 m) elevation [90]. In a 1990s survey of mature and old growth (>100 years) in the Washoe pine series, canopy cover of Washoe pine averaged 42% (range: 25%-75%), with mean canopy height of 62 feet (18.9 m). Cover of shrubs was slightly more than that of conifer saplings (22% and 13%, respectively); white fir dominated the sapling layer of fire-excluded sites. The herb layer was well developed (54% cover). Common to dominant shrubs included mountain big sagebrush, mountain snowberry, and pinemat manzanita. Common herbaceous species included bottlebrush squirreltail, Ross' sedge, western needlegrass, spreading phlox, and Sierra pea. A Washoe pine-white fir/tuber starwort association occurs in the south Warner Mountains, and a Washoe pine phase of the white fir series occurs from 6,200 to 7,200 feet (1,890-2,195 m) on north-facing aspects of the Warner Mountains. Washoe pine also occurs in the white fir/sweetcicely and white fir/tailcup lupine series [109].

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

GENERAL BOTANICAL CHARACTERISTICS

Botanical Description

This description covers characteristics that may be relevant to fire ecology and is not meant for identification. Washoe pine is distinguished from cooccurring varieties of ponderosa pine by its duller, gray-green needles, and from Jeffrey pine by its smaller cones [23]. Baldwin et al. [11] provide an identification key.

Washoe pine is short relative to other ponderosa pine varieties, generally <115 feet (35 m) tall and 5 feet (1.5 m) in diameter [11]. Its form is straight, with tapering branches. Ponderosa pine tends to self-prune, and fire also prunes lower branches [33]. Ponderosa pine bark is thick [66], although bark thickness of Washoe pine in particular was not documented as of 2018. The champion Washoe pine is on the Modoc National Forest; it measures 150 feet (46 m) in height, 17 feet (5 m) in circumference, and 75 feet (23 m) in crown spread [5]. Washoe pine needles are in bundles of three (rarely two) and 5 to 7 inches (12-17 cm long). They are thick and glaucous [11]. Female cones are oval and 2 to 5 inches (5-12 cm) long [11, 25], with closely-set scales. The seeds are large [23], with relatively short wings [23, 37, 55]. Immature cones are purple, a trait shared with ponderosa pine populations in Oregon and Washington [78].

Figure 3—Twigs and bark of Washoe pines on Mt. Rose, Nevada. ©2012 images by Gary A. Monroe, hosted by CalPhotos.

Presettlement stand structure of Washoe pine communities is not documented due to sparse early settlement and intensive logging. Northeastern California was not a popular route for settlers to travel [67]. Logging in the area from 1880 to the 1940s removed over 107 million board feet (25,000 m^3) of lumber, mostly pines [67].

Raunkiaer Life Form

Phanerophyte [86]

SEASONAL DEVELOPMENT

Washoe pine pollination occurs in July, cones mature from August to September, and seeds disperse in September. Seeds germinate in spring [61]. Individual ponderosa pine needles are retained for about 3 years [124], then shed in fall.

REGENERATION PROCESSES

Pollination and Breeding System

Washoe pine pollination is accomplished mostly by outcrossing, with some selfing. In field and shadehouse studies of four populations across Washoe pine's range, outcrossing rates were not significantly associated with aerial extent of the populations, population size, or population density ($P < 0.05$) [73]. A study of the Warner Mountain and Mt. Rose populations found heterozygosity of those populations was similar to that of *Pinus ponderosa* var. *ponderosa* populations in the same region [76].

Seed Production

Washoe pines first bear cones at 15 to 20 years of age. There are 2 to 5 years between large cone crops [61]. Cones take 2 years to mature [37].

The population on Mt. Rose, Nevada, has low seed viability. This may be due to inbreeding depression that occurred after most of the population was logged in the 19th century [23].

Seed Dispersal

Ponderosa pine seed is primarily dispersed by wind [8]. The winged seeds are somewhat buoyant and carry for short distances, usually no more than 150 feet (50 m) from the parent tree [50]. Dispersal is better downslope than on level ground or upslope [50].

Birds and mammals also disperse ponderosa pine seeds, and animal dispersal distances are often greater than those achieved by wind [19]. Clark's nutcrackers disperse and bury ponderosa pine seeds in shallow caches that contain a few seeds each [64, 65, 118]. Small mammals disperse ponderosa pine seeds either on the soil surface or in shallow caches [19]. Seeds buried by Clark's nutcrackers [64] or rodents have a greater chance of establishing than seeds dispersed by wind onto the forest floor [58].

Mosaic fires that create small openings help ensure that most of the burned landscape is within wind-dispersal distance of live ponderosa pines. Seed dispersal is limited to lacking on burns where large swaths of stand-replacement fire killed potential parent trees [57, 112]. Regeneration in centers of large, severe burns or clearcuts is generally poor because the seed does not travel into interior portions of the burn or clearcut [8, 72]. In Oregon, rate of ponderosa pine seed fall 120 feet (37 m) inside a clearing was only 22% of that at the edge of the clearing [13].

Seed Banking

Ponderosa pine has a short-term crown-stored seed bank [7, 107] and a short-term seed bank stored on the forest floor. Wind-dispersed seed overwinters in or on top of litter. Animal-cached seed may be stored in shallow soil seed banks. Ponderosa pine seed does not remain viable for longer than about 6 months in the field [103].

Germination

Seeds are dormant upon dispersal, requiring stratification [10], exposure to light [48, 68], or scarification [10] to break dormancy. Viable ponderosa pine seeds stratify naturally over winter and germinate the spring following dispersal [68, 102]. Light is not required for germination of overwintered seeds [68]. A laboratory study in British Columbia found that breaking the seed coat (scarification) of ponderosa pine seeds broke dormancy immediately; so did 1 to 2 months of late fall-winter stratification in a rough fescue grassland [10]. Germination is epigeal [77].

Seedling Establishment and Plant Growth

Ponderosa pine seedlings require open areas with mineral soil and quick access to lower soil layers [96]; thick litter and duff layers inhibit establishment [1, 3, 42, 101]. Openings larger than about 0.7 acre (0.3 ha) [53]—or overstory basal area of less than about 50 $feet^2$/acre (115 m^2/ha) [32]—are needed for substantial ponderosa pine seedling establishment. Light shade may increase seedling establishment of ponderosa pine on dry sites [40]. In the Warner Mountains, Washoe pine and other pines do not establish in late-successional Sierra lodgepole pine-white fir stands [89].

Mortality is high for ponderosa pine germinants and seedlings [59]. Primary causes of seedling mortality include fire (see Fire Effects), drought, browsing insects, browsing rodents and other mammals, fungi, frost, and heat [29, 38, 39, 104]. Ponderosa pine seedlings grow a long taproot to access lower soil layers before attaining much top growth [45, 77]. Course-textured soils can limit seedling establishment because those soils do not retain soil moisture well [30]. Ponderosa pine establishment is generally poor in dry years [108]. Regeneration pulses are associated with one or more consecutive wet years [82].

Prolonged drought is a major cause of death in ponderosa pines of all age classes [26, 28, 84]. Additionally, drought-stressed ponderosa pines are at increased risk to mortality from bark beetles [46].

Washoe pine's growth rate is slower than that of other varieties of ponderosa pine [87], likely due to the higher-elevation, harsher climate in which it grows [89]. On the Tahoe National Forest, Washoe pines reached breast height (4.5 feet (1.8 m)) at about 38 years of age. Trees on ridgetops and east-facing slopes had slowest growth rates, averaging 5 inches (13 cm) of growth annually. Washoe pines >100 years old averaged 44.3 feet (13.5 m) tall [116].

Ponderosa pines of all age classes respond to well release by low- to moderate-severity fire [4, 74, 99] (see Plant Response to Fire) or thinning [12, 29, 74, 98].

Vegetative Regeneration

Ponderosa pine does not naturally reproduce vegetatively [77].

SUCCESSIONAL STATUS

Washoe pine is shade intolerant [109]. Stands may be self-sustaining on harsh sites, but Washoe pine is seral to white fir and western white pine on northerly aspects and other mesic sites. Dominance is maintained in dry, harsh (e.g., serpentine) soils and/or by frequent- to moderate-interval surface fires [109] (see Fire Regimes). Smith [109] reports that in the Warner Mountains, Washoe pine maintains dominance on frequently burned sites, but white fir, Sierra lodgepole pine, and western white pine tend to replace Washoe pine successionally on long-unburned sites.

FIRE EFFECTS AND MANAGEMENT

In this review, low-severity fire is defined as fire that replaces <25% of the dominant overstory (i.e., ponderosa pine and any codominants); moderate-severity fire replaces 25% to 75% of the dominant overstory; and high-severity fire replaces >75% of the dominant overstory [14].

FIRE EFFECTS

Immediate Fire Effects on Plant

Fire Effects on Seeds

Crown fire or scorching kills seeds stored in ponderosa pine crowns [43]. Surface fire that occurs soon after seeds have dispersed likely kills Washoe pine seeds on the forest floor, although research on this was lacking as of 2018. Seeds stored in the cones of tall, fire- or self-pruned ponderosa pines generally survive low- and moderate-severity fires [108, 113].

Fire Effects on Trees

Fire resistance of Washoe pine and other varieties of ponderosa pine increases with tree age. Small ponderosa pines are susceptible to fire kill. Seedlings and saplings in dense stands are more susceptible to fire injury or death than young trees in open stands [3]. Although young ponderosa pines develop thick bark relatively quickly, they are still more susceptible to fire damage or mortality than older ponderosa pines with thicker bark [91]. Saplings and pole-sized ponderosa pines generally survive low-severity fires unless they are growing in dense stands, which can easily torch [7, 81]. Ponderosa pines 10 to 12 feet (3-4 m) tall generally survive moderate-severity surface fires [127]. Mature ponderosa pines survive low- [2, 17] and usually moderate-severity [2] fire. Crown fires kill ponderosa pines of all age classes [2, 8].

As long as the protected bud scales are not killed, mature ponderosa pines may survive 100% crown scorch [47, 121], although this is not common (see figure 4). For example, on the Colville Indian Reservation, Washington, damage from a wildfire to 30- to 40-year old ponderosa pines varied from almost no to 100% crown scorch. More small than large ponderosa pines died, but all ponderosa pines sustaining >95% crown scorch died [70]. Scorch damage incurred to ponderosa pines depends on height to needles and buds from the forest floor, stand density, and season of fire. Scorch damage is greater in dense than in open stands and generally, in summer and fall than in winter or spring [93, 117]. Ability of Washoe pine to survive substantial crown scorch is unknown.

Although fall fires generally cause more damage and mortality than spring prescribed fires (e.g., [93, 117]), this varies with ponderosa pine phenology and fire severity. Spring fire that occurs during or just after bud break can cause substantial damage to newly growing ponderosa pine tissues [115].

Hood and Lutes [51] provide a model to help predict ponderosa pine mortality from fire based on crown volume or crown length scorch, amount of dead cambium in the bole, and/or bark beetle attacks. The model is adapted for use across the West in FOFEM 6.0 [51].

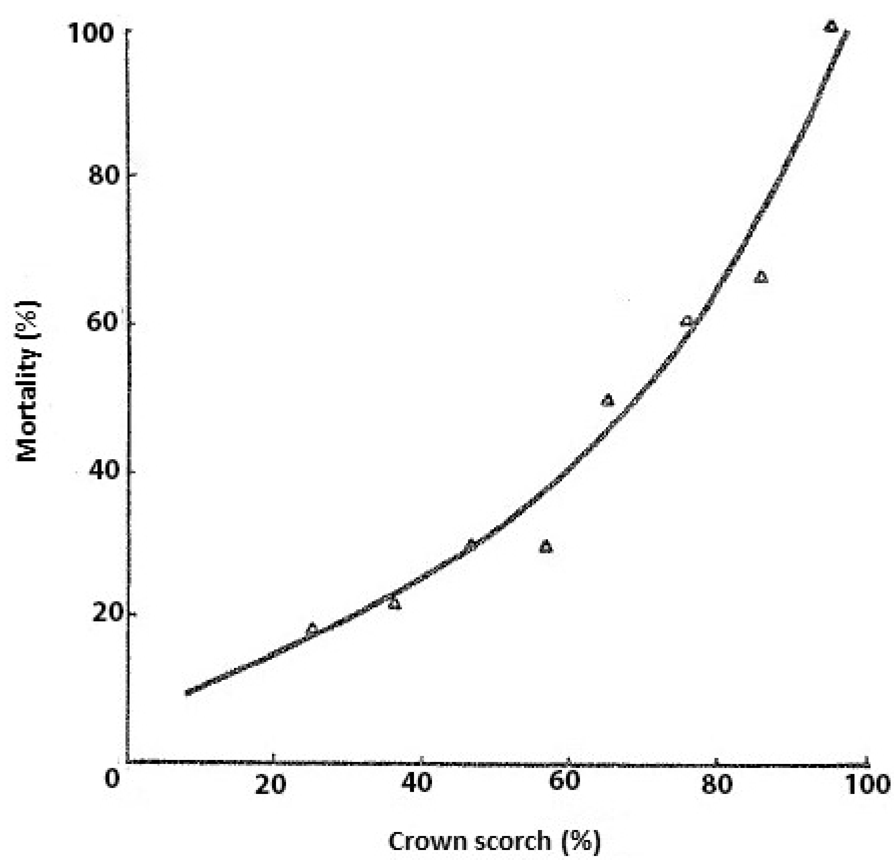

Figure 4—Mortality curve from crown scorch for mature ponderosa pines. Developed from postfire data collected on the Lolo National Forest, Montana. U.S. Forest Service image by Ryan [93].

Postfire Regeneration Strategy
Tree without adventitious buds and without a sprouting root crown
Crown residual colonizer (on site, initial community)
Initial off-site colonizer (off site, initial community)
Secondary colonizer (on- or off-site seed sources) [113]

FIRE ADAPTATIONS AND PLANT RESPONSE TO FIRE

Fire Adaptations

Ponderosa pine is adapted to low- and moderate-severity surface fires [4]. Adaptations to fire include thick bark; a high, open crown; self- and fire-pruned branches; large, scale-protected buds; high foliar moisture content; deep roots; and rapid root growth of seedlings [7, 35, 36, 93, 100]. During a fire, taxa with rough bark, such as Washoe pine, likely experience lower temperatures at the bark surface than taxa with smooth bark (review by [2]). The thick, platy, and fissured bark of mature ponderosa pines protects the cambium from low- and many moderate-severity fires [7]. Buds at branch tips are protected by bud scales [7, 94]. Trees with large buds, such as Washoe pine, are more resistant to fire damage than trees with small buds, such as white fir [93]. Branches of ponderosa pine are pruned by surface fires, lowering chances of torching [6].

Martin and Dell [71] report that at even in the seedling stage, ponderosa pines in the Inland West are more fire-resistant than seedlings of associated conifer species [7]. Ponderosa pine's resistance to fire damage increases with size [34].

Plant Response to Fire

Postfire Seedling Establishment and Growth

Ponderosa pine establishes from wind- and animal-dispersed seed after fire [63, 113]. Much of the seed comes from on-site sources: seed that disperses from crown-stored cones soon after the fire has passed [61, 113]. Wind-dispersed seeds typically fall within 150 feet (50 m) of the parent tree [7]. Seed dispersed by Clark's nutcrackers and small mammals can be a secondary source of postfire seedling establishment [63], and animals often disperse seed farther than wind. The Regeneration Processes section of this review provides details on ponderosa pine seed production, dispersal, and seedling establishment.

Mixed-severity burns where fire killed the overstory provide open patches in which ponderosa pine can establish [9, 20, 21, 27, 60]. Under favorable conditions, ponderosa pine seedlings establish in large numbers in early postfire years but thin over time [103].

Establishment of ponderosa pine can be poor on sites that experience large, stand-replacement fires. Severe fire generally kills on-site, crown-stored seeds. If open patches are too large, distance from off-site parent trees to burn interiors limits seed dispersal into burn interiors [8, 16, 30].

Mature Trees

Ponderosa pine growth tends to increase after low-severity fire and moderate-severity fire that caused little scorch damage [62, 121, 123]. However, some ponderosa pine stands—particularly after decades of fire exclusion—may show reduced growth after prescribed fire [105, 126] or wildfire [62] compared to prefire or unburned stands [126]. Early postfire recovery and growth rates of surviving ponderosa pines decrease with increasing crown scorch [74, 80, 114], although growth rates of scorched trees increase as needles grow completely back [94], which takes about 3 years [124]. Chances of recovery lessen if fire also damaged the bole and/or roots. Badly scorched trees may die within 1 or 2 postfire years, especially when fire is followed by drought and/or bark beetle attacks [95].

Managers speculate that because Washoe pine grows in harsher environments than other yellow pines, its responses to thinning and fire may differ from that of Jeffrey pine and other varieties of ponderosa pine [88, 89, 110]. As of 2018, however, research was lacking on what these differing responses might be. Riegel et al. [88] urge collaboration between land managers and researchers to develop an adaptive fire management program specific to Washoe pine.

Only one fire study investigating Washoe pine response to fire was available as of 2018. In that study, density of yellow pines (Washoe, Jeffrey, and ponderosa pine) after a wildfire on the Sagehen Experimental Forest north of Truckee, California, was greater than density of yellow pines in an adjacent unburned area. The 1960 Donner Ridge Fire burned about 44,500 acres (18,000 ha), some of which was a mixed-conifer forest with yellow pines and their hybrids. In postfire years 15 and 23, mean density of yellow pines was >3 times higher on burned plots than density of associated conifers, while basal area was similar. In contrast, density of yellow pines on unburned plots was less than density of associated conifers, while basal area was slightly higher (table 1) [85].

Table 1—Comparison of basal area [a] (m^2/ha) and density (stems/ha) of yellow pines and associated overstory species on burned and unburned plots following the 1960 Donner Ridge Fire. Data are means [85].

	Burned		Unburned	
	Postfire year 15 (1975)	Postfire year 23 (1983)	Postfire year 15 (1975)	Postfire year 23 (1983)
yellow pine complex [b]				
Basal area	3.1	4.4	24.2	30.1
Density	97.4	143.9	335.5	316.3
associated overstory conifers[c] (totaled for all species)				
Basal area	1.8	4.7	15.4	25.0
Density	25.7	39.2	457.2	384.2
associated overstory conifers by species				
red fir				
Basal area	0.2	0.3	1.4	0.7
Density	0.6	0.9	33.6	19.7
white fir				
Basal area	1.5	4.2	13.7	23.3
Density	3.9	9.2	415.2	381.3
Sierra lodgepole pine				
Basal area	0.1	0.2	0.0	0.0
Density	21.2	29.1	0.0	0.0
sugar pine				
Basal area	0.0	0.0	0.3	1.0
Density	0.0	0.0	8.4	13.2

[a]Only stems >2 m tall were included in basal area and density measures.
[b]Includes Washoe pine, Jeffrey pine, *Pinus ponderosa* var. *ponderosa*, and their hybrids.
[c]Includes red fir, white fir, Sierra lodgepole pine, and sugar pine.

FUELS AND FIRE REGIMES

Fuels

Fuels accumulate slowly in the upper montane zone of the Northeastern Plateau. Low fuel loads are the most limiting factor for fire occurrence. Needle litter and small twigs are the primary fuels [88, 89]. Riegel [90] et al. reported a mean depth of 2.1 inches (5.3 cm) (range = 0.5-5.0 inches (1.3-12.7) cm)) for the litter and duff layers of Washoe pine woodlands in the Warner Mountains. Continuity of surface fuels was variable, averaging 22% (range: 2%-65%) for shrubs and 54% (range: 35%-90%) for herbs [90].

Succession to shade-tolerant conifers has increased ladder fuels and total fuel loads in Washoe pine stands [89, 109, 116], increasing chances of crown fires. Riegel et al. [89] state that fire "helped regulate stand density and suppressed the continual recruitment of white fir". Standing dead fuels accumulate in beetle-kill patches and where yellow pines have died during the stem exclusion phase of succession to white fir [89].

Washoe pine stands were generally open at the time of European-American settlement [88]. Little is known of presettlement stand conditions, so comparing presettlement to current conditions is not possible [67].

Fire Regimes

Lightning is the primary ignition source for fires in Washoe pine communities. Lightning ignitions are common in Washoe pine's range [67]. For example, lightning frequently strikes the summit of Bald Mountain, where Washoe pine is dominant [109]. Fuels, not ignition source, limit fire occurrence [89]. On the Northeastern Plateau, lightning strikes occur from May through September but are most common from June through August (review by [88]).

Fire season runs from summer to early fall ([89, 122], Smith, unpublished data cited in [88]). A study in mixed-conifer forests in the Warner Mountains found fire season was mostly late summer to early fall: 90.6% of fire scars were at growing season-dormant season ring boundaries (fall); 7.8% were in latewood (late summer); and 1.6% in middle-earlywood (early summer) [89].

The fire regime of Washoe pine communities was not well documented as of 2018 [89]. Washoe pine communities may have fewer surface fires and longer fire intervals than communities of other varieties of ponderosa pine. Fire severity in ponderosa pine communities tends to become more mixed [56, 106], and fire intervals longer [2, 15, 18, 49, 92, 97, 111], with increasing elevation. Fire intervals lengthen due to a shorter growing season, more snowfall, less fuel accumulation, and moister fuels early in the fire season at high elevations [97].

Historically, fires in Washoe pine and mixed-pine communities were likely of mixed severity, with mostly low- to moderate-severity surface fires where pines dominated and stand-replacement fires where white fir was common in the subcanopy and/or canopy [88]. Small fire scars on the bases on Washoe pines in the Babbit Peak Research Natural Area, Tahoe National Forest, suggest that most fires were of low severity. Many Washoe pines in the area grow on rocky ridges where fires are likely infrequent [116]. Laudenslayer et al. [67] noted that on the Modoc National Forest, harvested pines (Washoe pine, Jeffrey pine, and ponderosa pine) were usually high-stumped 16 to 36 inches (41-91 cm) above ground due to fire scars below that height. This suggests a pattern of low- to moderate-severity surface fires.

Limited information suggests historical fire intervals were short to moderate fire in mixed-conifer forests on the Northeastern Plateau. A study in the Warner Mountains found mean composite fire intervals ranging from 3.5 to 40 years from 1746 to 1957. The study was conducted in the upper montane, mixed-conifer zone, but it was unclear whether or not Washoe pine occurred on the study site. Sierra lodgepole pine was present, along with white fir and western white pine (reviews by [88, 89]).

A dendrochrological study on the Sagehen Experimental Forest found a median composite fire interval of 7 years (range: 1-41 years, time frame: 1700-2006) in relatively low-elevation (6,306-6,768 ft (1,922-2,063 m)) Jeffrey pine stands. Washoe pine did not occur in the 900-acre (360-ha) study site [120], although it occurs in the experimental forest (refer to table 1 and text just above the table) [120].

On high-elevation, cold sites, Washoe pine can maintain dominance without fire for long periods. A survey on Bald Mountain showed little white fir regeneration 30 to 40 years after wildfire [109]. Jeffrey pine-Washoe pine alliances on strongly serpentine soils are considered self-replacing [75]. The soils are so restrictive to other conifers that fire may not be needed to perpetuate these stands.

Smith [109] speculated that high-elevation Washoe pine woodlands historically burned in a mosaic pattern. At the landscape level, surface fires maintained Washoe pine in many patches, while white fir and Sierra lodgepole pine dominated long-unburned patches [109].

Information on presettlement fire sizes in Washoe pine communities was lacking as of 2018. A study on the Modoc National Forest suggests that fire sizes were small in the settlement period. Sixty-four wildfires were recorded between 1910 and 1919. Although they burned a total of 212,652 acres (86,057 ha), only two of those fires were >2,000 acres (800 ha). Occurrence of those fires was not broken down by forest type (review by [88]).

Find further fire regime information for the plant communities in which Washoe pine occurs by entering “Washoe pine” in the FEIS home page under "Find Fire Regimes".

FIRE MANAGEMENT CONSIDERATIONS

Fire exclusion has led to an increase of white fir at the expense of Washoe pine [90]. Washoe pine stands are vulnerable to stand-replacement fire in areas where white fir has established in the understory [88, 89]. Washoe pine-white fir associations are particularly susceptible to successional replacement by white fir and other shade-tolerant species [88, 89, 109]. Riegel et al. [88] noted that the fire regime in the upper montane zone of the Northeastern Plateau region—where Washoe pine grows—has been the least affected by fire exclusion of all the mixed-conifer types. However, they acknowledge the potential for an altered fire regime (stand-replacement fire) in Washoe pine stands where white fir has established [89].

MANAGEMENT CONSIDERATIONS

FEDERAL LEGAL STATUS

None

OTHER STATUS

NatureServe ranks Washoe pine’s conservation status as G3, vulnerable and rare. The Washoe pine woodland alliance is ranked G1: critically imperiled due to disjunct occurrences and threats from logging [75].

IMPORTANCE TO WILDLIFE AND LIVESTOCK

Within its limited range, Washoe pine provides important wildlife habitat. Great gray owls [109], northern goshawks [109, 116], and mountain lions [116] are among the wildlife species that use Washoe pine communities.

As of 2018, no information was available on Washoe pine’s palatability, nutritional value, or cover value for wildlife and livestock; its value for restoration/rehabilitation; or other uses. The FEIS review on *Pinus ponderosa* var. *benthamiana-P. p.* var. *ponderosa* provides information on closely related varieties of ponderosa pine.

OTHER MANAGEMENT CONSIDERATIONS
Primary threats to Washoe pine include successional replacement under fire exclusion and loss of habitat due to climate change [88].

APPENDIX

Table A1—Common and scientific names of plant species mentioned in this review. Links go to FEIS Species Reviews.

Common name	Scientific name
Trees	
California red fir	*Abies magnifica*
coast Douglas-fir	*Pseudotsuga menziesii* var. *menziesii*
giant chinquapin	*Chrysolepis chrysophylla*
incense-cedar	*Calocedrus decurrens*
Jeffrey pine	*Pinus jeffreyi*
ponderosa pine	*Pinus ponderosa*
Columbia ponderosa pine, Pacific ponderosa pine	*Pinus ponderosa* var. *ponderosa*, *Pinus ponderosa var. benthamiana*
Rocky Mountain ponderosa pine, southwestern ponderosa pine	*Pinus ponderosa* var. *scopulorum*, *Pinus ponderosa* var. *brachyptera*
Washoe pine	*Pinus ponderosa* var. *washoensis* (this review)
Sierra lodgepole pine	*Pinus contorta* var. *murrayana*
singleleaf pinyon	*Pinus monophylla*
western white pine	*Pinus monticola*
whitebark pine	*Pinus albicaulus*
white fir	*Abies concolor*
Shrubs	
antelope bitterbrush	*Purshia tridentata*
curlleaf mountain-mahogany	*Cercocarpus ledifolius*
dwarf ceanothus	*Ceanothus pumilus*
greenleaf manzanita	*Arctostaphylos patula*
mountain big sagebrush	*Artemisia tridentata* subsp. *vaseyana*
mountain snowberry	*Symphoricarpos oreophilus*
pinemat manzanita	*Arctostaphylos nevadensis*
snowbrush ceanothus	*Ceanothus velutinus*
wedgeleaf ceanothus	*Ceanothus cuneatus*
Graminoids	
Idaho fescue	*Festuca idahoensis*
prairie Junegrass	*Koeleria macrantha*
Ross' sedge	*Carex rossii*
rough fescue	*Festuca campestris*
squirreltail	*Elymus elymoides*
western needlegrass	*Achnatherum occidentale*
Wheeler bluegrass	*Poa nervosa*
Forbs	
common beargrass	*Xerophyllum tenax*
common yarrow	*Achillea millefolium*

sweetcicely	*Osmorhiza berteroi*
tailcup lupine	*Lupinus caudatus*
tuber starwort	*Pseudostellaria jamesii*
Sierra pea	*Lathyrus nevadensis*
spreading phlox	*Phlox diffusa*
woolly mule-ears	*Wyethia mollis*

REFERENCES

1. Acton, Suzanne. 2003. Fire severity and salvage logging effects on exotics in ponderosa pine dominated forests. In: Omi, Philip N.; Joyce, Linda A., tech. eds. Fire, fuel treatments, and ecological restoration: Conference proceedings; 2002 April 16-18; Fort Collins, CO. Proceedings RMRS-P-29. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 445. Abstract. [45340]

2. Agee, James K. 1993. Fire effects on vegetation. In: Agee, James K. Fire ecology of Pacific Northwest forests. Washington, DC: Island Press: 113-150. [90488]

3. Agee, James K. 1993. Ponderosa pine and lodgepole pine forests. In: Agee, James K. Fire ecology of Pacific Northwest forests. Washington, DC: Island Press: 320-250. [90494]

4. Agee, James K. 1998. Fire and pine ecosystems. In: Richardson, David M., ed. Ecology and biogeography of Pinus. Cambridge, United Kingdom: The Press Syndicate of the University of Cambridge: 193-218. [37704]

5. American Forests. 2018. Champion trees national register, [Online]. Washington, DC: American Forests (Producer). Available: http://www.americanforests.org/explore-forests/americas-biggest-trees/champion-trees-national-register/. [92568]

6. Arno, Stephen F. 1977. The stately ponderosa. Pacific Search. 11(10): 24-25. [15812]

7. Arno, Stephen F. 1988. Fire ecology and its management implications in ponderosa pine forests. In: Baumgartner, David M.; Lotan, James E., comps. Ponderosa pine: The species and its management: Symposium proceedings; 1987 September 29 - October 1; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 133-139. [9410]

8. Arno, Stephen F.; Fiedler, Carl E. 2005. Chapter 3: Knowledge from historical fire regimes. In: Arno, Stephen F.; Fiedler, Carl E., eds. Mimicking nature's fire: Restoring fire-prone forests in the West. Washington, DC: Island Press: 14-28. [69055]

9. Arno, Stephen F.; Smith, Helen Y.; Krebs, Michael A. 1997. Old growth ponderosa pine and western larch stand structures: Influences of pre-1900 fires and fire exclusion. Res. Pap. INT-RP-495. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 20 p. [30083]

10. Bai, Yuguang; Thompson, Don; Broersma, Klaas. 2004. Douglas fir and ponderosa pine seed dormancy as regulated by grassland seedbed conditions. Journal of Range Management. 57(6): 661-667. [23948]

11. Baldwin, Bruce G.; Goldman, Douglas H.; Keil, David J.; Patterson, Robert; Rosatti, Thomas J.; Wilken, Dieter H., eds. 2012. The Jepson manual. Vascular plants of California, second edition. Berkeley, CA: University of California Press. 1568 p. [86254]

12. Barrett, James W. 1970. Ponderosa pine saplings respond to control of spacing and understory vegetation. Res. Pap. PNW-106. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 16 p. [15815]

13. Barrett, James W. 1979. Silviculture of ponderosa pine in the Pacific Northwest: The state of our knowledge. Gen. Tech. Rep. PNW-97. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 196 p. [7306]

14. Barrett, S.; Havlina, D.; Jones, J.; Hann, W.; Frame, C.; Hamilton, D.; Schon, K.; Demeo, T.; Hutter, L.; Menakis, J. 2010. Interagency fire regime condition class guidebook (FRCC), [Online], (Version 3.0). In: Interagency fire regime condition class website. U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior; The Nature Conservancy (Producers). Available: https://www.frames.gov/files/7313/8388/1679/FRCC_Guidebook_2010_final.pdf [2017, March 1]. [85876]

15. Barrett, Stephen W. 1983. Fire history of the River of No Return Wilderness. Part 1: Colson Creek study area, Salmon National Forest. Progress Report. Missoula, MT: Systems for Environmental Management. 5 p. On file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Laboratory, Missoula, MT. [17372]

16. Bonnet, V. H.; Schoettle, A. W.; Shepperd, W. D. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Canadian Journal of Forest Research. 35: 35-47. [55606]

17. Busse, Matt D.; Simon, Steve A.; Riegel, Gregg M. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned Pinus ponderosa forests of central Oregon. Forest Science. 46(2): 258-268. [42058]

18. Cairns, David M.; Butler, David R.; Malanson, George P. 2002. Geomorphic and biogeographic setting of the Rocky Mountains. In: Baron, Jill S., ed. Rocky Mountain futures: An ecological perspective. Washington, DC: Island Press: 27-39. [45443]

19. Chambers, Jeanne C.; MacMahon, James A. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics. 25: 263-292. [67827]

20. Chambers, Marin E.; Fornwalt, Paula J.; Malone, Sparkle L.; Battaglia, Mike A. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine-dominated forests of the Colorado Front Range. Forest Ecology and Management. 378: 57-67. [91066]

21. Collins, Brandon M.; Roller, Gary B. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecology. 28(9): 1801-1813. [87559]

22. Conkle, M. Thompson; Critchfield, William B. 1988. Genetic variation and hybridization of ponderosa pine. In: Baumgartner, David M.; Lotan, James E., comps. Ponderosa pine: The

species and its management: Symposium proceedings; 1987 September 29 - October 1; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 27-43. [9399]

23. Critchfield, William B. 1984. Crossability and relationships of Washoe pine. Madrono. 31(3): 144-170. [21749]

24. Critchfield, William B.; Little, Elbert L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p. [20314]

25. Cronquist, Arthur; Holmgren, Arthur H.; Holmgren, Noel H.; Reveal, James L. 1972. Intermountain flora: Vascular plants of the Intermountain West, U.S.A. Vol. 1. New York: Hafner Publishing Company, Inc. 270 p. [717]

26. Daubenmire, R. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology. 49(3): 431-438. [12942]

27. Dickman, Alan. 1978. Reduced fire frequency changes species composition of a ponderosa pine stand. Journal of Forestry. 76(1): 24-25. [8000]

28. Dodson, Erich Kyle; Root, Heather Taylor. 2013. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in ponderosa pine forest, Oregon, USA. Forest Ecology and Management. 302: 163-170. [86990]

29. Dolph, K. Leroy; Mori, Sylvia R.; Oliver, William W. 1995. Long-term response of old-growth stands to varying levels of partial cutting in the Eastside pine type. Western Journal of Applied Forestry. 10(3): 101-108. [26520]

30. Donato, Daniel C; Fontaine, Joseph B.; Campbell, John L.; Robinson, W. Douglas; Kauffman, J. Boone; Law, Beverly E. 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Canadian Journal of Forest Research. 39(4): 823-838. [81544]

31. Farjon, Aljos. 1998. World checklist and bibliography of conifers. 2nd ed. Kew, England: The Royal Botanic Gardens. 309 p. [61059]

32. Fiedler, Carl E. 1999. Tree response: Stand structure in response to selection cutting and burning. In: Smith, Helen Y.; Arno, Stephen F., eds. Eighty-eight years of change in a managed ponderosa pine forest. Gen. Tech. Rep. RMRS-GTR-23. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 31-34. [38288]

33. Fiedler, Carl E.; Arno, Stephen F. 2015. A special tree. In: Ponderosa: People, fire and the West's most iconic tree. Missoula, MT: Mountain Press Publishing: 40-57. [89315]

34. Filip, Gregory M. 2005. Diseases as agents of disturbance in ponderosa pine. In: Ritchie, Martin W.; Maguire, Douglas A.; Youngblood, Andrew, tech. coords. Proceedings of the symposium on ponderosa pine: Issues, trends, and management; 2004 October 18-21; Klamath Falls, OR. Gen. Tech. Rep. PSW-GTR-198. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 227-232. [65973]

35. Fischer, William C.; Bradley, Anne F. 1987. Fire ecology of western Montana forest habitat types. Gen. Tech. Rep. INT-223. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 95 p. [633]

36. Flint, H. R. 1925. Fire resistance of northern Rocky Mountain conifers. U.S. Department of Agriculture, Forest Service, Applied Forestry Note 61. Missoula, MT: Northern Rocky Mountain Forest Experiment Station. 5 p. [34634]

37. Flora of North America Editorial Committee, eds. 2018. Flora of North America north of Mexico, [Online]. Flora of North America Association (Producer). Available: http://www.efloras.org/flora_page.aspx?flora_id=1. [36990]

38. Forrestel, Alison B.; Andrus, Robert A.; Fry, Danny L.; Stephens, Scott L. 2017. Fire history and forest structure along an elevational gradient in the southern Cascade Range, Oregon, USA. Fire Ecology. 13(1): 1-15. [91664]

39. Fowells, H. A.; Stark, N. B. 1965. Natural regeneration in relation to environment in the mixed conifer forest type of California. Res. Pap. PSW-24. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 14 p. [15642]

40. Geier-Hayes, Kathleen. 1987. Occurrence of conifer seedlings and their microenvironments on disturbed sites in central Idaho. Res. Pap. INT-383. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 12 p. [3554]

41. Goldman, Doug. 2015. [Personal communication with Janet Fryer]. August 28. Regarding taxonomy of ponderosa pine. Greensboro, NC: U.S. Department of the Interior, Natural Resource Conservation Service. On file with: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [89372]

42. Graham, Russell T.; Jain, Theresa B. 2005. Ponderosa pine ecosystems. In: Ritchie, Martin W.; Maguire, Douglas A.; Youngblood, Andrew, tech. coords. Proceedings of the symposium on ponderosa pine: Issues, trends, and management; 2004 October 18-21; Klamath Falls, OR. Gen. Tech. Rep. PSW-GTR-198. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 1-32. [65908]

43. Griffin, James R. 1982. Pine seedlings, native ground cover, and Lolium multiflorum on the Marble-Cone burn, Santa Lucia Range, California. Madrono. 29(3): 177-188. [4935]

44. Griffin, James R.; Critchfield, William B. 1972. The distribution of forest trees in California. Res. Pap. PSW-82. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 118 p. [1041]

45. Grulke, Nancy E.; Retzlaff, William A. 2001. Changes in physiological attributes of ponderosa pine from seedling to mature tree. Tree Physiology. 21(5): 275-286. [37141]

46. Guarin, Alejandro; Taylor, Alan H. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. Forest Ecology and Management. 218(1-3): 229-244. [68689]

47. Hanson, Chad T.; North, Malcolm P. 2009. Post-fire survival and flushing in three Sierra Nevada conifers with high initial crown scorch. International Journal of Wildland Fire. 18(7): 857-864. [81077]

48. Harrington, Michael. 1977. Response of ponderosa pine seeds to light. Res. Note INT-220. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p. [12599]

49. Heyerdahl, Emily K.; Lertzman, Ken; Karpuk, Stephen. 2007. Local-scale controls of a low severity fire regime (1750-1950), southern British Columbia, Canada. Ecoscience. 14(11): 40-47. [67919]

50. Hofmann, J. V. 1917. The relation of brush fires to natural reproduction. Unpublished report. On file with: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Lab, Missoula, MT. 32 p. [+ photographs]. [26805]

51. Hood, Sharon; Lutes, Duncan. 2017. Predicting post-fire tree mortality for 12 western US conifers using the First-Order Fire Effects Model (FOFEM). Fire Ecology. 13(2): 66-84. [92328]

52. ITIS Database. 2018. Integrated taxonomic information system, [Online]. Available: http://www.itis.gov/index.html. [51763]

53. Kane, Van R.; North, Malcolm P.; Lutz, James A.; Churchhill, Derek J.; Roberts, Susan L.; Smith, Douglas F.; McGaughey, Robert J.; Kane, Jonathan T.; Brooks, Matthew L. 2014. Assessing fire effects on forest spatial structure using a fusion of Landsat and airborne LiDAR data in Yosemite National Park. Remote Sensing of Environment. 151: 89-101 [+ appendices]. [89243]

54. Kartesz, J. T. The Biota of North America Program (BONAP). 2015. Taxonomic Data Center, [Online]. Chapel Hill, NC: The Biota of North America Program (Producer). Available: http://www.bonap.net/tdc. [Maps generated from Kartesz, J. T. 2010. Floristic synthesis of North America, Version 1.0. Biota of North America Program (BONAP). [in press]. [84789]

55. Kartesz, John Thomas. 1988. A flora of Nevada. Reno, NV: University of Nevada. 1729 p. Dissertation. [42426]

56. Kaufmann, Merrill R.; Ryan, Kevin C.; Fule, Peter Z.; Romme, William H. 2005. Restoration of ponderosa pine forests in the interior western U.S. after logging, grazing, and fire suppression. In: Stanturf, John A.; Madsen, Palle, eds. Restoration of boreal and temperate forests. New York: CRC Press: 481-500. [54685]

57. Kemp, Kerry B. 2015. Wildfire and climate change in mixed-conifer ecosystems of the northern Rockies: Implications for forest recovery and management. Moscow, ID: University of Idaho. 153 p. [+ appendices]. Dissertation. [90228]

58. Keyes, Christopher R.; Acker, Steven A.; Greene, Sarah E. 2001. Overstory and shrub influences on seedling recruitment patterns in an old-growth ponderosa pine. Northwest Science. 75(3): 204-210. [40178]

59. Keyes, Christopher. R.; Maguire, Douglas A.; Tappeiner, John C. 2007. Observed dynamics of ponderosa pine (Pinus ponderosa var. ponderosa Dougl. ex Laws.) seedling recruitment in the Cascade Range, USA. New Forests. 34(1): 95-105. [68634]

60. Keyser, Tara L.; Lentile, Leigh B.; Smith, Frederick W.; Shepperd, Wayne D. 2008. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. Forest Science. 54(3): 328-338. [74237]

61. Krugman, Stanley L.; Jenkinson, James L. 2008. Pinus L.: pine. In: Bonner, Franklin T.; Karrfalt, Robert P., eds. Woody plant seed manual. Agric. Handbook No. 727. Washington, DC: U.S. Department of Agriculture, Forest Service: 809-874. [68019]

62. Landsberg, J. D.; Cochran, P. H.; Finck, M. M.; Martin, R. E. 1984. Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine. Res. Note PNW-412. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 13 p. [4976]

63. Lanner, Ronald M. 1983. Trees of the Great Basin: A natural history. Reno, NV: University of Nevada Press. 215 p. [1401]

64. Lanner, Ronald M. 1996. Other arrangements. In: Lanner, Ronald M. Made for each other: A symbiosis of birds and pines. New York: Oxford University Press: 55-60. [29921]

65. Lanner, Ronald M. 1998. Seed dispersal in Pinus. In: Richardson, David M., ed. Ecology and biogeography of Pinus. Cambridge, UK: The Press Syndicate of the University of Cambridge: 281-295. [37707]

66. Lanner, Ronald M. 1999. Conifers of California. Los Olivos, CA: Cachuma Press. 274 p. [30288]

67. Laudenslayer, William F., Jr.; Darr, Herman H.; Smith, Sydney. 1989. Historical effects of forest management practices on eastside pine communities in northeastern California. In: Tecle, Aregai; Covington, W. Wallace; Hamre, R. H., tech. coords. Multiresource management of ponderosa pine forests: Proceedings of the symposium; 1989 November 14-16; Flagstaff, AZ. Gen. Tech. Rep. RM-185. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 26-34. [11305]

68. Li, X. J.; Burton, P. J.; Leadem, C. L. 1994. Interactive effects of light and stratification on the germination of some British Columbia conifers. Canadian Journal of Botany. 72(11): 1635-1646. [24594]

69. Little, Elbert L., Jr. 1975. Rare and local conifers in the United States. Conservation Research Rep. No. 19. Washington, DC: U.S. Department of Agriculture, Forest Service. 25 p. [15691]

70. Lynch, Donald W. 1959. Effects of a wildfire on mortality and growth of young ponderosa pine trees. Res. Note No. 66. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p. [4748]

71. Martin, Robert E. 1982. Shrub control by burning before timber harvest. In: Baumgartner, David M., comp. Site preparation and fuels management on steep terrain: Proceedings of a

symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 35-40. [18528]

72. McDonald, Philip M. 1980. Seed dissemination in small clearcuttings in north-central California. Res. Pap. PSW-150. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 5 p. [7913]

73. Mitton, J. B.; Latta, R. G.; Rehfeldt, G E. 1997. The pattern of inbreeding in Washoe pine and survival of inbred progeny under optimal environmental conditions. Silvae Genetica. 46(4): 215-219. [28615]

74. Morris, William G.; Mowat, Edwin L. 1958. Some effects of thinning a ponderosa pine thicket with a prescribed fire. Journal of Forestry. 56: 203-209. [8109]

75. NatureServe. 2018. International ecological classification standard: Terrestrial ecological classifications, [Online]. In: NatureServe Central Databases. Arlington, VA: NatureServe (Producer). Available: http://explorer.natureserve.org/servlet/NatureServe?init=Ecol [2018, September 19]. [87721]

76. Niebling, Charles R.; Conkle, M. Thompson. 1990. Diversity of Washoe pine and comparisons with allozymes of ponderosa pine races. Canadian Journal of Forest Research. 20(3): 298-308. [15841]

77. Oliver, William W.; Ryker, Russell A. 1990. Pinus ponderosa Dougl. ex Laws. ponderosa pine. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America. Volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 413-424. [13399]

78. Patten, Ann M. 1999. A molecular phylogenetic analysis of Pinus, section Diploxylon, subsection Ponderosae: Interspecific and intraspecific genetic relationships. Moscow, ID: University of Idaho. 99 p. [33079]

79. Patten, Ann M.; Brunsfeld, Steven J. 2002. Evidence of a novel lineage within the Ponderosae. Madrono. 49(3): 189-192. [43901]

80. Pearson, H. A.; Davis, J. R.; Schubert, G. H. 1972. Effects of wildfire on timber and forage production in Arizona. Journal of Range Management. 25(4): 250-253. [5664]

81. Peterson, David W.; Hessburg, Paul F.; Salter, Brion; James, Kevin M.; Dahlgreen, Matthew C.; Barnes, John A. 2007. Reintroducing fire in regenerated dry forests following stand-replacing wildfire. In: Powers, Robert F., tech. ed. Restoring fire-adapted ecosystems: Proceedings of the 2005 national silvicultural workshop; 2005 June 6-10; Tahoe City, CA. Gen. Tech. Rep. PSW-GTR-203. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 79-86. [68607]

82. Peterson, David W.; Kerns, Becky K.; Dodson, Erich K. 2014. Using model projections. In: Peterson, David W.; Kerns, Becky K.; Dodson, Erich K. Climate change effects on vegetation in the Pacific Northwest: A review and synthesis of the scientific literature and simulation model

projections. Gen. Tech. Rep. PNW-GTR-900. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 95-98. [90576]

83. Peterson, Eric B. 2008. International vegetation classification alliances and associations occurring in Nevada with proposed additions. Carson City, NV: Nevada Natural Heritage Program. 347 p. Available online: http://heritage.nv.gov/sites/default/files/library/ivclist.pdf [2018, January 10]. [77864]

84. Puhlick, Joshua J.; Laughlin, Daniel C.; Moore, Margaret M. 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. Forest Ecology and Management. 264(1): 10-19. [84149]

85. Raphael, Martin G.; Morrison, Michael L.; Yoder-Williams, Michael P. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. The Condor. 89: 614-626. [6873]

86. Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Oxford, England: Clarendon Press. 632 p. [2843]

87. Rehfeldt, G. E. 1999. Systematics and genetic structure of Washoe pine: Applications in conservation genetics. Silvae Genetica. 48(3-4): 167-173. [36275]

88. Riegel, Gregg M.; Miller, Richard F.; Skinner, Carl N.; Smith, Sydney E. 2006. Northeastern Plateaus bioregion. In: Sugihara, Neil G.; van Wagtendonk, Jan W.; Shaffer, Kevin E.; Fites-Kaufman, Joann; Thode, Andrea E., eds. Fire in California's ecosystems. Berkeley, CA: University of California Press: 225-263. [65541]

89. Riegel, Gregg M.; Miller, Richard F.; Skinner, Carl N.; Smith, Sydney E.; Farris, Calvin A.; Merriam, Kyle E. 2018. Northeastern Plateaus region. In: van Wagtendonk, Jan W.; Sugihara, Neil G.; Stephens, Scott L.; Thode, Andrea E.; Shaffer, Kevin E.; Fites-Kaufman, Jo Ann, eds. Fire in California's ecosystems. 2nd ed. Oakland, CA: University of California Press: 219-248. [92957]

90. Riegel, Gregg M.; Thornburgh, Dale A.; Sawyer, John O. 1990. Forest habitat types of the South Warner Mountains, Modoc County, California. Madrono. 37(2): 88-112. [11466]

91. Rigolot, E.; Ducrey, M.; Duhoux, F.; Huc, R.; Ryan, K. C. 1994. Effects of fire injury on the physiology and growth of two pine species. In: 2nd international conference on forest fire research: Proceedings: Vol. 2; 1994 November 21-24; Coimbra, Portugal. Coimbra, Portugal: Domingos Xavier Viegas, ADAI: Associacao para o Desenvolvimento da Aerodinamica Industrial: 857-866. [26404]

92. Rollins, Matthew G.; Swetnam, Thomas W.; Morgan, Penelope. 2001. Evaluating a century of fire patterns in two Rocky Mountain wilderness areas using digital fire atlases. Canadian Journal of Forest Research. 31(12): 2107-2123. [84633]

93. Ryan, Kevin C. 1982. Evaluating potential tree mortality from prescribed burning. In: Baumgartner, David M., ed. Site preparation and fuels management on steep terrain: Proceedings of a symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 167-179. [5616]

94. Ryan, Kevin C. 1982. Techniques for assessing fire damage to trees. In: Lotan, James E., ed. Fire--its field effects; Proceedings of the symposium; 1982 October 19-21; Jackson, WY. Missoula, MT: The Intermountain Fire Council; Pierre, SD: The Rocky Mountain Fire Council: 1-11. [10986]

95. Ryan, Kevin C. 2000. Effects of fire injury on water relations of ponderosa pine. In: Moser, W. Keith; Moser, Cynthia F., eds. Fire and forest ecology: Innovative silviculture and vegetation management: Proceedings of the 21st Tall Timbers fire ecology conference: An international symposium; 1998 April 14-16; Tallahassee, FL. No. 21. Tallahassee, FL: Tall Timbers Research: 58-66. [37611]

96. Ryker, Russell A.; Losensky, Jack. 1983. Ponderosa pine and Rocky Mountain Douglas-fir. In: Burns, Russell M., tech. comp. Silvicultural systems for the major forest types of the United States. Agric. Handb. 445. Washington, DC: U.S. Department of Agriculture, Forest Service: 53-55. [16904]

97. Safford, Hugh D.; Van de Water, Kip M. 2014. Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. Res. Pap. PSW-RP-266. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 60 p. [89431]

98. Sala, Anna; Peters, Gregory D.; McIntyre, Lorna R.; Harrington, Michael G. 2005. Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. Tree Physiology. 25(3): 339-348. [53345]

99. Saveland, James M. 1982. Predicting mortality and scorch height in ponderosa pine from understory prescribed burning. Moscow, ID: University of Idaho. 39 p. Thesis. [6481]

100. Saveland, James M.; Bunting, Stephen C. 1988. Fire effects in ponderosa pine forests. In: Baumgartner, David M.; Lotan, James E., comps. Ponderosa pine: The species and its management: Symposium proceedings; 1987 September 29 - October 1; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 125-131. [9409]

101. Schultz, A. M.; Biswell, H. H. 1959. Effect of prescribed burning and other seedbed treatments on ponderosa pine seedling emergence. Journal of Forestry. 57: 816-817. [850]

102. Shearer, Raymond C. 1975. Seedbed characteristics in western larch forests after prescribed burning. Res. Pap. INT-167. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 26 p. [12342]

103. Shearer, Raymond C. 1989. Fire effects on natural conifer regeneration in western Montana. In: Baumgartner, David M.; Breuer, David W.; Zamora, Benjamin A.; Neuenschwander, Leon F.; Wakimoto, Ronald H., comps. Prescribed fire in the Intermountain region: Forest site preparation and range improvement: Symposium proceedings; 1986 March 3-5; Spokane, WA. Pullman, WA: Washington State University, Department of Natural Resources, Cooperative Extension: 19-33. [11242]

104. Shearer, Raymond C.; Schmidt, Wyman C. 1970. Natural regeneration in ponderosa pine forests of western Montana. Res. Pap. INT-86. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 19 p. [15795]

105. Simon, Steven A. 1990. Fire effects from prescribed underburning in central Oregon ponderosa pine plant communities: First and second growing season after burning. In: Proceedings, Pacific Northwest range management short course: Fire in Pacific Northwest ecosystems; 1990 January 23-25; Pendleton, OR. Corvallis, OR: Oregon State University, Department of Rangeland Resources: 93-109. [92343]

106. Skinner, Carl N.; Abbott, Celeste S.; Fry, Danny L.; Stephens, Scott L.; Taylor, Alan H.; Trouet, Valerie. 2009. Human and climatic influences on fire occurrence in California's North Coast Range, USA. Fire Ecology. 5(3): 76-99. [81120]

107. Smith, Helen Y. 2000. Factors affecting ponderosa pine snag longevity. In: Pioneering new trails: Proceedings of the Society of American Foresters 1999 national convention; 1999 September 11-15; Portland, OR. SAF Publication 00-1. Bethesda, MD: Society of American Foresters: 223-229. [37560]

108. Smith, Jane Kapler; Fischer, William C. 1997. Fire ecology of the forest habitat types of northern Idaho. Gen. Tech. Rep. INT-GTR-363. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 142 p. [27992]

109. Smith, Sydney. 1994. Ecological guide to Eastside pine plant associations, northeastern California: Modoc, Lassen, Klamath, Shasta-Trinity, Plumas, and Tahoe National Forests. R5-ECOL-TP-004. Vallejo, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region. 174 p. [65647]

110. Smith, Syndey. 2018. [Personal communication to Janet Fryer]. June 12. Regarding Washoe pine. Alturas, CA: U.S. Department of Agriculture, Forest Service, Modoc National Forest [Retired]. On file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT; FEIS files. [92967]

111. Soeriaatmadja, Roehajat Emon. 1966. Fire history of the ponderosa pine forests of the Warm Springs Indian Reservation, Oregon. Corvallis, OR: Oregon State University. 123 p. Dissertation. [44325]

112. Stevens, Jens T. S.; Collins, Brandon M.; Miller, Jay D.; North, Malcolm P.; Stephens, Scott L. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. Forest Ecology and Management. 406: 28-36. [92345]

113. Stickney, Peter F. 1989. Seral origin of species comprising secondary plant succession in northern Rocky Mountain forests. FEIS workshop: Postfire regeneration. Unpublished draft on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT. 10 p. [20090]

114. Sutherland, Elaine Kennedy. 1988. Prescribed burning and ponderosa pine growth: What managers should know. In: Baumgartner, David M.; Lotan, James E., comps. Ponderosa pine: The species and its management: Symposium proceedings; 1987 September 29-October 1; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension; 280-281. Abstract. [9430]

115. Swezy, D. Michael; Agee, James K. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research. 21(5): 626-634. [15551]

116. Talley, Steven N.; Keeler-Wolf, Todd. 2004. Babbit Peak. In: Cheng, Sheauchi. tech. ed. Forest Service Research Natural Areas in California. Gen. Tech. Rep. PSW-GTR-188. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture: 22-25. [92970]

117. Thies, Walter G.; Niwa, Christine G.; Westlind, Douglas J. 2001. Impact of prescribed fires in ponderosa pine stands in the southern Blue Mountains on various components of the ecosystem--three years post fire. In: Marshall, Katy, comp. Proceedings, 49th western international forest disease work conference; 2001 September 10-14; Carmel, CA. Corvallis, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 108-112. [64787]

118. Tomback, Diana F. 2001. Clark's nutcracker: Agent of regeneration. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: Ecology and restoration. Washington, DC: Island Press: 88-104. [36698]

119. USDA Natural Resources Conservation Service. 2018. PLANTS Database, [Online]. U.S. Department of Agriculture, Natural Resources Conservation Service (Producer). Available: https://plants.usda.gov. [34262]

120. Vaillant, Nicole M.; Stephens, Scott L. 2009. Fire history of a lower elevation Jeffrey pine-mixed conifer forest in the eastern Sierra Nevada, California, USA. Fire Ecology. 5(3): 4-19. [81116]

121. Van Sickle, F. S.; Hickman, R. D. 1959. The effect of understory competition on the growth rate of ponderosa pine in north central Oregon. Journal of Forestry. 57: 852-853. [4608]

122. van Wagtendonk, Jan W.; Sugihara, Neil G.; Stephens, Scott L.; Thode, Andrea E.; Shaffer, Kevin E.; Fites-Kaufman, Jo Ann. 2018. Appendix one: Fire regime attributes for each vegetation type discussed in the bioregional chapters. In: van Wagtendonk, Jan W.; Sugihara, Neil G.; Stephens, Scott L.; Thode, Andrea E.; Shaffer, Kevin E.; Fites-Kaufman, Jo Ann, eds. Fire in California's ecosystems. 2nd ed. Oakland, CA: University of California Press: 523-527. [92969]

123. Weaver, Harold. 1957. Effects of prescribed burning in ponderosa pine. Journal of Forestry. 55: 133-137. [4619]

124. Weidman, R. H. 1939. Evidences of racial influence in a 25-year test of ponderosa pine. Journal of Agricultural Research. 59(12): 855-887. [91952]

125. Willyard, Ann; Gernandt, David S.; Potter, Kevin; Hipkins, Valerie; Marquardt, Paula; Mahalovich, Mary Frances; Langer, Stephen K.; Telewski, Frank W.; Cooper, Blake; Connor, Douglas; Finch, Kristen; Karemera, Hassani H.; Lefler, Julia; Lea, Payton; Wofford, Austin. 2017. Pinus ponderosa: A checkered past obscured four species. American Journal of Botany. 104(1): 161-181. [91547]

126. Wooldridge, David D.; Weaver, Harold. 1965. Some effects of thinning a ponderosa pine thicket with a prescribed fire, II. Journal of Forestry. 63: 92-95. [4622]

127. Wright, Henry A. 1978. The effect of fire on vegetation in ponderosa pine forests: A state-of-the-art review. Lubbock, TX: Texas Tech University, Department of Range and Wildlife Management. 21 p. In cooperation with: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. [64181]