Pinus ponderosa var. benthamiana, P. p. var. ponderosa: Ponderosa pine 2018

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Figure 1—Dr. Steve Arno by an Indian-peeled ponderosa pine that burned in 2003 (Bartlett Mountain Fire) in the Bob Marshall Wilderness, Montana. U.S. Forest Service image by Robert Keane.

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ABSTRACT

This Species Review covers two varieties of ponderosa pine, *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa*. "Ponderosa pine" refers to both varieties.

Ponderosa pine adapted to dry environments but occupies a wide variety of sites. It dominates or codominates low-elevation, dry forests and tends to form savannas in which there are few or no other tree species on xeric sites. It grows with other overstory trees on more mesic sites and at midelevations.

Ponderosa pine regenerates most successfully after disturbances that open the canopy and expose bare mineral soil. Fire is the primary agent creating these conditions. Seed production varies within and among populations and between years. Wind and animals disperse the seeds. Few seeds actually establish. For those that do, growth is most favorable on open sites with light shade, such as sites that have been burned or thinned.

Ponderosa pine is shade intolerant. It is a successionally stable or climax species on low-elevation, dry sites and seral on more mesic and midelevation sites. Under fire exclusion, many contemporary ponderosa pine forests have denser stand structures than the forests had historically. Live and dead fuels have increased as shade-tolerant species replace ponderosa pine successionally.

Ponderosa pine is adapted to low- and moderate-severity surface fires. Effects of fire generally vary with tree age and fire severity. Low-severity surface fire usually kills ponderosa pine seedlings, while saplings and pole-sized trees generally survive. Ponderosa pines over 10 to 12 feet (3-4 m) tall usually survive moderate-severity surface fires. Fall fires generally cause more injury and mortality than spring fires. Postfire mortality may be delayed for several years and may be exacerbated by drought and bark beetle attacks.

Ponderosa pine establishes from wind- and wildlife-dispersed seed in open patches where fire killed overstory trees. If open patches are too big, distance from off-site parent trees limits seed dispersal into burn interiors. Regeneration can be poor on sites that experience stand-replacement fire, especially when fires are large.

Historically, fire maintained ponderosa pine as a dominant throughout its range. Before European settlement around the mid-1850s, low-elevation, dry ponderosa pine and dry ponderosa pine-Douglas-fir forests had mostly frequent, low- and moderate-severity surface fires and mixed-severity fires. Historical fire intervals in ponderosa pine forests were generally short—averaging about 10 years—but ranged from 1 to 80 years across the ranges of *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa*. Fires became infrequent when fire exclusion became effective in the 1930s.

Ponderosa pine ecosystems historically experienced both small and large fires, but large patches of severe fire were uncommon. In recent decades, the proportion of area that has burned at high severity has increased in ponderosa pine forests across ponderosa pine's range. This has been attributed primarily to successional advancement under fire exclusion and climate change. Frequent low- to moderate-severity fires can reduce fuel loads and kill young conifers in the understory; reduce mortality of mature ponderosa pines from subsequent fires; help restore reference-condition forest structure and composition; promote regeneration of shade-intolerant conifers; and increase resilience of dry forest ecosystems.

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INTRODUCTION

FEIS ABBREVIATIONS

PINPON
PINPONE
PINPONP

COMMON NAMES

For *Pinus ponderosa*, the species:
ponderosa pine
western yellow pine

For *Pinus ponderosa* var. *benthamiana:*
Pacific ponderosa pine

For *Pinus ponderosa* var. *ponderosa*:
Columbia ponderosa pine
Douglas's ponderosa pine
North Plateau ponderosa pine

TAXONOMY

The scientific name of ponderosa pine is *Pinus ponderosa* Lawson & Lawson (Pinaceae) [53, 132, 133, 184, 307, 350, 550]. This review covers two varieties of ponderosa pine:

Pinus ponderosa var. *benthamiana*
Pinus ponderosa var. *ponderosa*

The taxonomy of ponderosa pine is in flux [207, 589], with the accepted number and nomenclature of ponderosa pine infrataxa in dispute (see Synonyms). Varieties of ponderosa pine are distinguished by genetics, morphology, and geographical location [123, 307, 550]. Generally accepted varieties include:

Pinus ponderosa var. *benthamiana* (Hartw.) Vasey, Pacific ponderosa pine
Pinus ponderosa var. *brachyptera* (Engelm.) Lemmon, southwestern ponderosa pine [550]
Pinus ponderosa var. *ponderosa* C. Lawson, Columbia ponderosa pine [53, 307, 550]
Pinus ponderosa var. *scopulorum* Engelm., Rocky Mountain ponderosa pine
Pinus ponderosa var. *washoensis* (H. Mason & Stockw.) J.R. Haller & Vivrette, Washoe pine [307, 550].

Callaham [105] recognizes a sixth entity, *Pinus ponderosa* subsp. *readiana* Callaham, called central high plains ponderosa pine. Arizona pine (*Pinus arizonica* Engelm.) is sometimes classified as a variety of ponderosa pine [184] but is usually classified as a separate species [307, 550, 589].

Most systematists did not distinguish between *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa* until the early 2010s, and some still consider them synonyms [161]. Most literature does not distinguish between the two varieties, so in this review, "ponderosa pine" refer to both varieties. Common name usage is not consistent for the varieties: until the mid-2010s, *Pinus ponderosa* var. *ponderosa* was usually referred to as "Pacific ponderosa pine", not "Columbia ponderosa pine". Because common name usage has been inconsistent, the varieties of ponderosa pine discussed in this review are referred to by their scientific names.

Hybrids

Varieties of ponderosa pine hybridize freely where their ranges overlap. *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa* hybridize with Jeffrey pine and Coulter pine, although rarely [123, 132, 226, 422]. Different pollination times usually restrict hybridization between those pine taxa [422].

See table A1 for a complete list of common and scientific names of plant species discussed in this synthesis and links to other FEIS Species Reviews.

SYNONYMS

For *Pinus ponderosa* var. *benthamiana:*
Pinus benthamiana Hartw. [589]
Pinus ponderosa var. *pacifica* J.R. Haller & Vivrette [53, 307]
Pinus ponderosa subsp. *critchfieliana* Callaham [105]

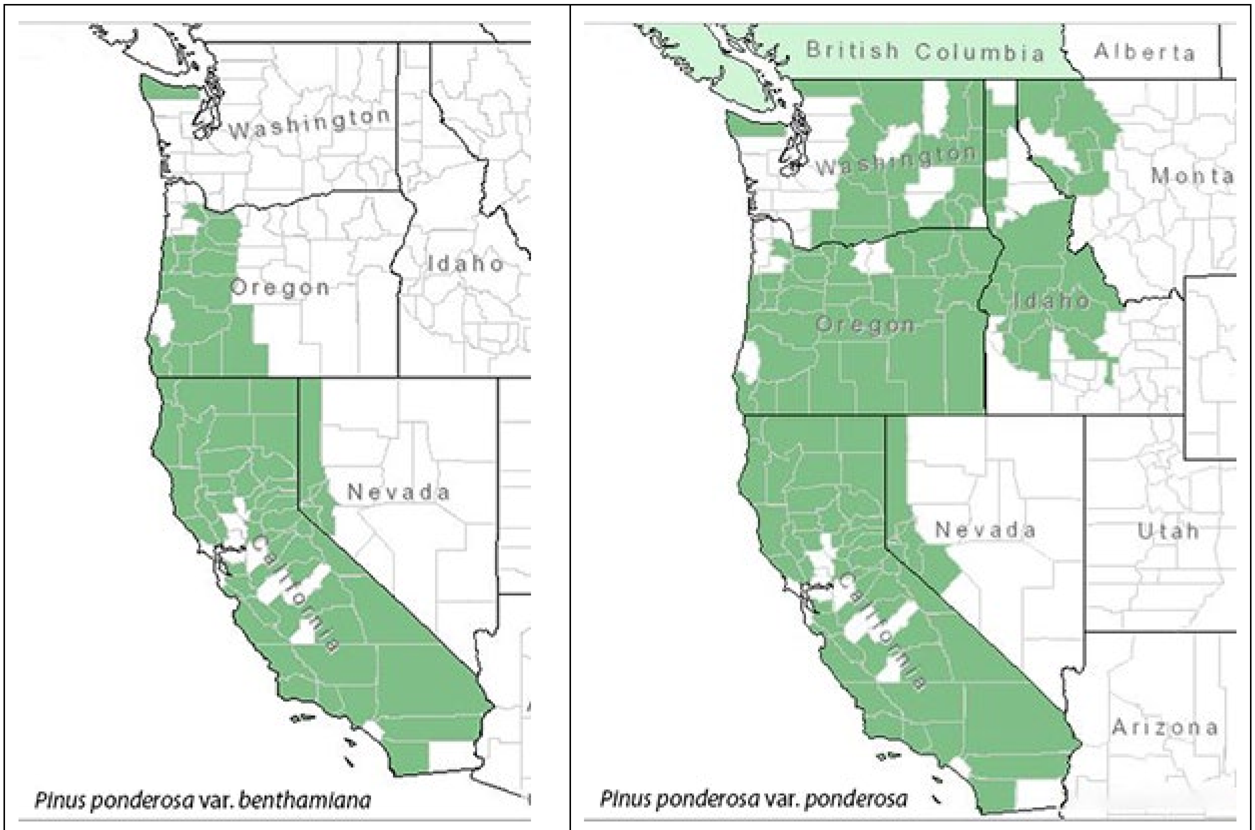
For *Pinus ponderosa* var. *ponderosa*:
Pinus ponderosa subsp. *ponderosa* [105]

LIFE FORM

Tree

DISTRIBUTION AND PLANT COMMUNITIES

GENERAL DISTRIBUTION


Pinus ponderosa var. benthamiana

Pinus ponderosa var. ponderosa

Figure 2—Distributions of *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa* in the United States. Maps courtesy of USDA, NRCS. 2017. The PLANTS Database. National Plant Data Team, Greensboro, NC. [2018, March 06] [550].

Ponderosa pine is native to western North America. Next to lodgepole pine, it is the most widely distributed conifer in North America [132, 212]. *Pinus ponderosa* var. *benthamiana* occurs mainly in the Pacific states. Its core distribution is from northwestern Oregon south to southern California [132, 550]. Isolated populations occur in Clallam County, Washington [550]. *Pinus ponderosa* var. *ponderosa* is widely distributed across the West. It occurs from western Montana and central Idaho [132, 550] west to interior southern British Columbia [277] and south to west-central Nevada and southern California [132, 550]. Distributions of *P. p.* var. *benthamiana*, *P. p.* var. *ponderosa*, and *P. p.* var. *washoensis* overlap in the Pacific states, and distributions of *P. p.* var. *ponderosa* and *P. p.* var. *scopulorum* overlap in central Idaho and western Montana [132, 497, 550]. Intermediate forms and hybrids occur where distributions of the varieties overlap [497].

States and Provinces
Pinus ponderosa var. *benthamiana*:
United States: CA, NV, OR, WA [550]

Pinus ponderosa var. *ponderosa*:
United States: CA, ID, MT, NV, OR, WA [550]
Canada: BC [277, 550]

SITE CHARACTERISTICS AND PLANT COMMUNITIES

Site Characteristics

Ponderosa pine is widely adapted to a variety of environments [202, 422], from dry, desert-like mesas and plateaus to wet bottomlands [292, 422]. It is one of the most drought-tolerant tree species in North America [422] and is considered an indicator of dry forest environments [20, 417]. Common garden studies using ponderosa pines from widely different climates suggest that ponderosa pine has broad genetic tolerance to drought across populations [378, 450, 600]. It is also tolerant of frost, high temperatures [417], and fire (see Fire Adaptations). However, its resistance to freezing is low relative to conifers that grow at higher elevations [475].

Pinus ponderosa var. *benthamiana* grows in modified maritime [57] and mediterranean [349] climates. *Pinus p.* var. *ponderosa* grows in continental [466], modified maritime [57], and mediterranean [349] climates. An interior continental climate occurs east of the Cascade crest [466]; a modified maritime climate in the Coast Ranges of Washington and northern Oregon and on the west slope of the Cascade Range [57]; and a mediterranean climate in southwestern Oregon and throughout ponderosa pine's range in California [349]. In the Northern Rocky and Blue mountains, the interior continental climate is somewhat moderated by ocean air masses; this effect fades as distance from the coast increases [141]. Genetic studies show *P. p.* var. *ponderosa* is strongly associated with wet winter climates ($R^2 = 0.78$), while *P. p.* var. *scopulorum* is associated with wet summer climates ($R^2 = 0.62$) [497].

Ponderosa pine grows on moist to dry sites [209]. It has "fairly high" flood resistance; it grows on alluvial sites that flood in spring [344] and is often a component of riparian vegetation [25, 34, 350]. Mean annual precipitation in ponderosa pine communities ranges from 10 to 50 inches (250-1,270 mm). In western Montana, mean annual precipitation in ponderosa pine communities ranges from 15 to 30 inches (380-760 mm)/year (review by [551]); in northern California, from 30 to 50 inches (760-1,270 mm)/year [378, 450, 600].

Ponderosa pine grows in many different soil types, in soils derived from igneous, metamorphic, and sedimentary substrates [57, 82, 422, 551]. It grows in gabbro [14] and other ultramafic soils [291]. Although typically absent on serpentine soils [212], it has been reported on serpentine soils in El Dorado County, California [593]. It grows in soils of many textural classes—from clays [87, 551] to sands [212, 551]—but grows best in coarse-textured loams and moderately sandy or gravelly soils (review by [551]). Soil pH in ponderosa pine stands varies from very strongly acidic to very strongly alkaline (pH 4.9-9.1), but usually ranging from slightly acidic to neutral (pH 6.0-7.0) in upper soil horizons [422].

Ponderosa pine grows in foothill and low-elevation mountain zones [202]. Topography is highly variable; ponderosa pine stands occupy level plateaus, gentle slopes, and steep canyon walls [202]. In mixed-conifer forests, ponderosa pine often occupies dry, south- and west-facing slopes, while Douglas-fir and other more mesophytic species occupy north- and east-facing slopes. In foothills surrounding the Willamette Valley of Oregon, for example, ponderosa pine historically grew on south slopes, while Douglas-fir grew on north slopes [119].

Ponderosa pine grows at progressively higher elevations and in narrower vegetation zones from north to south [422]. In the Pacific Northwest, it is most common between 1,500 to 4,000 feet (450-1,200 m) elevation [34], while in southern California it occurs above 7,000 feet (2,000 m) [226, 422, 551] (table 1). It tends to grow at higher elevations on south- than on north-facing slopes. In western Montana, for example, ponderosa pine reaches its highest elevation, 6,200 feet (1,900 m), on south-facing slopes [34].

Table 1—Elevational ranges of ponderosa pine.

Area	Range
British Columbia	1,000-4,000 feet (3,00-1,200 m) [277, 551]
Northern Rocky Mountains	1,000-6,000 feet (300-2,000 m) [417, 422, 466]
Montana	3,200-6,200 feet (1,000-1,900 m) [45, 439]
Washington	0-4,000 feet (0-1,220 m) [422]
Blue Mountains, Oregon	1,600-,5000 feet (500-1,520 m) [422, 551]
south-central Oregon pumice zone	4,800-6,600 feet (1,460-2,010 m) [422]
western Oregon	1,200-5,220 feet (370-1,590 m) [2, 45, 558]
northern California	500-6,000 feet (150-2,000 m) [226, 417, 422, 551]
southern California	5,000-7,300 feet (1,60-2,200 m) [226, 422, 551]

In California, *Pinus ponderosa* var. *benthamiana* grows as low as 500 feet (150 m) along drainages of the Sacramento River [212]. *Pinus p.* var. *ponderosa* occurs from 1,000 to 2,000 (300-600 m) in the Klamath Mountains, 1,500 to 3,500 feet (450-1065 m) and the northern Sierra Nevada, and from 5,300 to 7,300 feet (1,600-2200 m) in the southern Sierra Nevada [421].

Plant Communities

Background: Ponderosa pine is the largest forest cover type in the West [202]. Site characteristics—including available soil water, topographic position, and aspect—greatly influence the degree of its overstory dominance in dry and mixed-conifer forests [202, 300, 417]. In this review, “mixed conifer” refers to mixed-conifer communities in which ponderosa pine is a dominant or important component of the vegetation.

Ponderosa pine communities generally form a band between lower-elevation, dry grassland, shrubland, or hardwood (often oak) communities and higher-elevation, mixed-conifer forests [4, 466]. Since it is highly drought tolerant, ponderosa pine is often the first tree encountered above xeric steppe vegetation [9, 34, 140].

- Plant Communities by Region
- Stand Structure

Plant Communities by Region

In the **Northern Rocky Mountains**, ponderosa pine dominates low-elevation dry sites and is seral in Douglas-fir and midelevation mixed-conifer communities. Rocky Mountain juniper sometimes codominates at low elevations. Associates at midelevations (~4,000-5,000 feet (1,200-1,500 m)) include grand fir, Rocky Mountain Douglas-fir, Rocky Mountain lodgepole pine, and western larch [234, 300, 439]. In western Montana, ponderosa pine-perennial bunchgrass savannas and woodlands tend to occur on stony, coarse-textured, or shallow soils, while ponderosa pine/shrub forests tend to occur on deeper, finer-textured soils. Bluebunch wheatgrass and Idaho fescue commonly dominate the grass component of savannas and woodlands; antelope bitterbrush and mallow ninebark often dominate shrub understories [128, 140, 348, 439].

Ponderosa pine dominates some riparian communities of the Northern Rocky Mountains. These communities, usually imbedded in a drier ponderosa pine zone, have large overstory ponderosa pines, with cottonwoods and willows growing alongside. Western larch may codominate at midelevations. The understory is typically a diverse assemblage of shrubs, including Douglas hawthorn, Greene's mountain-ash, and Saskatoon serviceberry. In late-seral stands, suppressed grand fir is often present in understories and subcanopies. The ground layer a diverse assemblage of herbaceous species, some of which are rare on uplands [25, 34, 235, 350].

In the **Pacific Northwest**, ponderosa pine dominates low-elevation savannas, woodlands, forests, and some riparian communities. In savannas and woodlands, bluebunch wheatgrass, Idaho fescue, and needle-and-thread grass frequently dominant the ground layer. Antelope bitterbrush, mallow ninebark, and common snowberry are frequently dominant shrubs in forest communities. Some stands have both a ground layer of bunchgrasses and/or sedges and understory shrubs ([141]; review by [4]). Ponderosa pine codominates some Oregon white oak communities of Washington and Oregon. Shrub dominants in these communities include buckbrush and sticky whiteleaf manzanita [130].

Ponderosa pine is a common associate in mixed-conifer forests of the Pacific Northwest. Coast Douglas-fir typically dominates, with canyon live oak, California black oak, Pacific madrone, sugar pine, and tanoak frequent overstory associates. Pacific poison-oak and dwarf rose typically dominate or are common in the shrub layer [45].

In eastern Washington, ponderosa pine/common snowberry riparian associations occur on alluvial deposits along seasonal or perennial streams. Stand structure is typically open-grown, mature ponderosa pines with a shrub understory. Lewis’ mock orange and Saskatoon serviceberry are common [131].

In the Blue Mountains, ponderosa pine dominates low-elevation dry woodlands and forests and codominates with Rocky Mountain Douglas-fir in mixed-conifer forests. Historically, perennial bunchgrasses dominated the ground layer of dry ponderosa pine communities and shrubs were infrequent. Bluebunch wheatgrass, Idaho fescue, and Ross’ sedge are common groundlayer dominants [294].

In **California**, ponderosa pine historically dominated low-elevation woodlands and forests and cooccurred in mixed-conifer forests at midelevations. It codominates with grey pine in low-elevation woodlands that border chaparral [87]. In ponderosa pine and Sierran mixed-conifer forests, it occurs with coast Douglas-fir, incense-cedar, sugar pine, and white fir [417, 507, 561]. Sierra or western juniper may codominate on dry sites [507]. Ponderosa pine associates with Jeffrey pine in some mixed-conifer forests [82, 142], although Jeffrey pine tends to displace ponderosa pine on cold sites, serpentine and other ultramafic soils, and at mid- to upper elevations of the mixed-conifer zone [349]. In the Transverse and Peninsular ranges, ponderosa pine associates with bigcone Douglas-fir and Coulter pine [82, 142].

Oaks and other hardwoods associate with ponderosa pine throughout ponderosa pine's range in California. At low elevations, ponderosa pine grows with interior live oak and canyon live oak. At midelevations, it grows with California black oak and tanoak. Ponderosa pine grows with Oregon white oak and Pacific madrone in northern California [87, 507].

In the southern Cascade Range, ponderosa pine occurs in mixed-conifer forests with Douglas-fir, sugar pine, and white fir. Bigleaf maple, canyon live oak, and California black oak often codominate the overstory. These forests may be mosaicked with montane chaparral, and chaparral species such as greenleaf manzanita and ceanothus are common in the understory. Western juniper and curlleaf mountain-mahogany cooccur with ponderosa pine on dry slopes in the East Cascades (review by [506]).

East of the Cascades in northeastern California, ponderosa pine grows in dry forests and woodlands. It often cooccurs with western juniper. Greenleaf manzanita, antelope bitterbrush, Bloomer goldenbush, and/or greenleaf manzanita are dominant shrubs. Idaho fescue and/or western needlegrass often dominate the ground layer [156].

Mountain misery an important understory shrub of dry forests throughout much of the southern Cascades and Sierra Nevada. Other important or dominant shrubs include buckbrush, greenleaf manzanita, and sticky whiteleaf manzanita [561].

Stand Structure

Summary: Historically, ponderosa pine grew in mostly open stands of mature and old-growth trees, with scattered patches of younger ponderosa pines. Successive fires often produced a mosaic of different-aged stands across the landscape. Past logging, fire exclusion, and successional advancement have resulted in increases in stand density and compositional shifts to shade-tolerant conifers.

On xeric sites, ponderosa pine tends to form savannas in which there are few or no other tree species. On more mesic sites, it forms woodlands and forests in a mix with other overstory trees [9]. Stands subject to frequent fire typically have widely spaced trees (review by [5]). However, ponderosa pine forests were historically structurally diverse, and many remain so today. A mix of fire severities creates fine-grained spatial heterogeneity across dry forest landscapes [305, 359, 472]. Open patches were historically common on sites that experienced mixed-severity fires [359].

Pioneer accounts, old photographs, and General Land Office and early timber survey data indicate that ponderosa pine cover types historically had open, parklike stand structure [31, 221, 223], with small patches of conifer seedlings and saplings [245, 248] (generally ≤50-foot (15-m) diameter patches) [249]. Arno [30] reports that historically, trees were typically spaced at least 25 feet (8 m) apart in ponderosa pine stands across the West. An 1889 U.S. Geological Survey report of ponderosa pine stands in eastern Washington stated that ponderosa pine "growth is never dense, and on the dry hillsides of this region it is quite scattering, but constitutes about 85 per cent of the trees growing" [208].

Historically, ponderosa pine cover types dominated about 20% of forested landscapes. Accounts from settlers in the Pacific Northwest describe open ponderosa pine stands. Upon encountering presettlement forests (1853-1855) on the East Cascades in Washington, a settler wrote "There is so little underbrush in these forests that a wagon may be drawn through them without difficulty…The level terraces, covered everywhere with good grass and shaded by fine symmetrical trees of great size, through whose open, light foliage the sun's rays penetrate with agreeable mildness, give these forests an appearance of an ornamental park" (Cooper 1960, cited in [167]). An 1853 account of the Blue Mountains described "beautiful groves of pine trees…The country is all burned over, so often there is not the least underbrush, but the grass grows thick and beautiful" (Evans 1990, cited in [33]). Historical data from unlogged portions of the Klamath Indian Reservation in south-central Oregon indicate that from 1919 to 1922, large ponderosa pines (>21 inches (53 cm) DBH) dominated both dry forest and mesic mixed-conifer habitat types [223].

On many sites, historical structure of ponderosa pine riparian communities might have been similar to that of upland ponderosa pine communities. Studies reconstructing historical stand structure of riparian ponderosa pine forest communities in eastern Washington [594], the southern Blue Mountains of Oregon [423], and the southern Cascades of California [556] found that stand structure was not substantially different between riparian and upland forests. This was attributed to similar fire regimes for riparian and upland forests [556].

Figure 3—A ponderosa pine/pinegrass woodland on Meeks Table Research Natural Area, Washington. The area has never been logged or grazed and retains its presettlement stand structure. U.S. Forest Service photo.

Age class structure of ponderosa pine communities may be even- or uneven-aged, depending on landscape scale, fire history, other site history, and site characteristics such aspect and soil moisture [578]. Seedling establishment after fire often results in even-aged patches, so age class tends to be similar within individual young patches. Successive fires and other disturbances (e.g., insect outbreaks and windfall [186, 536]) result in a mosaic of different-aged patches across the landscape [9, 209]. Individual patches become increasingly uneven-aged over time [596] due to gap succession [9] and the establishment of shade-tolerant trees between successive fires. Localized bark beetle attacks, for example, create openings in mature ponderosa pine stands, allowing for gap succession [9, 25]. On the Lolo National Forest of Montana, stand reconstruction of pre-1900 ponderosa pine-western larch stands showed a predominately uneven-aged structure (*n* = 7 stands). One stand was even-aged; the authors attributed this to cohort establishment after a stand-replacement fire in the early 1700s [42].

Studies of mature and old-growth ponderosa pine stands in Oregon and California found both even- and uneven-aged structure. In eastside old-growth ponderosa pine stands at Metolius Research Natural Area, central Oregon, ponderosa pines grew in even-aged patches. However, old-growth ponderosa pines farther south at Pringle Butte Research Natural Area grew in uneven-aged patches [596]. A fire history study in Ishi Wilderness on the Lassen National Forest, California, found that prior to 1905, individual ponderosa pine patches were even-aged, but patches were of different ages across the landscape due to fine-scale differences in fire history [536]. On Blacks Mountain Experimental Forest on the Lassen National Forest, 1933-1934 inventories documented uneven-aged stand structure. The stands were about 89% ponderosa pine, with more ponderosa pines on valley bottoms than on upland slopes [456]. See table A2 for detailed information on stand structure of ponderosa pine stands in Oregon and California.

Snags are an important component of ponderosa pine communities; they may remain upright for more than a century [9]. Snag management is discussed in Fire Management Considerations (Snags section) and Old Growth and Snags for Wildlife.

Stand structure has changed greatly in most ponderosa pine forests since historical times, with dense, young stands of shade-tolerant conifers replacing widely spaced old growth due to logging of large trees and long periods of fire exclusion [42, 223]. Across the West, over 90% of ponderosa pine forests have been heavily logged at least once, and most iconic, old-growth trees were harvested. Fiedler [168] reports that “second-growth stands typify the modern forest, and on perhaps half of the land originally dominated by large, old ponderosas, firs are replacing the younger pines”.

Surveys of unlogged portions of the Klamath Indian Reservation revealed dramatic changes in stand structure of conifer forests over 87 years (table A3). Stand densities in a 1997-2006 survey were three times those of a 1919-1922 survey. Although mean basal area increased by nearly 20%, basal area of large conifers declined by 50%, and the proportion of large trees was more than 5 times less than in the early survey [223].

Equations are available to help predict these structural components of ponderosa pine stands:

- crown width and weight of foliage, developed from stands in northern Idaho and western Montana [406]; and
- height based on DBH. Basal area and site index can be incorporated in to the equations as independent variables; developed from mixed-conifer stands in southwestern Oregon [358].

Identifying old growth can help guide management planning and vegetation inventories. Proposed standards for classifying a ponderosa pine stand as old growth include:

- the stand is dominated by ponderosa pines >16 inches (40 cm) DBH and >200 years old;
- it has high between-patch structural diversity; patches are typically 0.2 to 4.9 acres (0.08-2.0 ha);
- it contains conifer snags ≥20 inches (50 cm) DBH and >15 feet (4.6 m) tall at a density of ≥3 snags/acre (7/ha); and
- it contains moderate to extensive woody debris, with logs at a density of ≥10 tons/acre (22 t/ha) including at least 2 logs/acre (5/ha) that are ≥24 inches (61 cm) diameter and >50 feet (15 m) long [190, 309]. Woody debris load is variable, however, depending on fire frequency [5].

Fiedler et al. [171] recommend using both structural and functional (e.g., vigor and diversity indices) attributes to help identify and monitor old-growth ponderosa pine stands.

Harrod et al. [247] provide a model for estimating historical snag density in dry forests of the East Cascades. See the Snags and Old Growth and Snags for Wildlife sections of this review for detailed information on snag management.

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. Identification keys are available for distinguishing *Pinus ponderosa* var. *benthamiana* from *P. p.* var. *ponderosa* where their distributions overlap ([53, 105]); however, positive identification is challenging because these varieties hybridize and characteristics used to distinguish the two varieties overlap.

Ponderosa pine is a large tree with long needles and thick bark [133]. Form is straight, with a slightly tapering bole [53, 82]. Heights of 90 to 130 feet 928-40 m) and DBH of 30 to 50 inches (80-130 cm) are common [34, 88]. On favorable sites, trees in Idaho and western Montana have attained diameters of 4 feet (1 m) and in California, of 6 feet (2 m) [209]. The champion tree, a *Pinus ponderosa* var. *ponderosa* in Oregon, is 167 feet (51 m) tall, 29 feet (9 m) in circumference, 9.2 feet (2.8 m) in diameter, and 68 feet (21 m) in crown spread [17].

The bark of mature ponderosa pines is platy, rough, and scaly [2, 357]. It has low density and exfoliates readily [480]. Thickness may equal or exceed 3.0 inches (7.6 cm) [357]. In 1921, Jepson [292] reported ponderosa pines with 5-inch (12.7-cm) thick bark in the Sierra Nevada.

Ponderosa pine branches are thick, spreading [11, 168], and tufted at the ends [9]. Branches are few and open on boles in open stands, but branches on boles in closed stands may be crowded [2]. Fire prunes lower branches in stands subject to frequent fires [34]. Ponderosa pine tends to self-prune [2], although some open-grown trees on unburned sites may have branches nearly reaching the ground [16].

Needles of *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa* are in bundles of three, and 5 to 10 inches (13-25 cm) long [350, 422]. They are clustered in tufts at branch tips [9]. *Pinus ponderosa* var. *benthamiana* tends to have longer, thinner, more flexible needles than *P. p.* var. *ponderosa* [123].

Female (seed) cones are oval and 3 to 6 inches (8-15 cm) long [350, 422]—about the size of a fist—and armed with prickles [167]. Seeds are winged [53].

The taproot and large roots of ponderosa pine are deep on favorable sites, making trees windfirm [350]. In sand or other porous soils, large roots may extend 6 feet (2 m) deep or more, but are rarely more than 3 feet (1 m) deep in heavy clay soil (review by [422]).

Fine roots are typically shallow and short-lived. A study in Washington found that 74% of fine ponderosa pine roots infected with ectomycorrhizae were in mineral soil at depths of ≤2 inches (5 cm) [253]. In the Boise Basin on the Boise National Forest, Idaho, most fine roots were concentrated below the humus layer, in mineral soil [152]. An Oregon study found fine roots of ponderosa pine lived about 1 year. Young trees had the largest proportion of fine roots at shallow soil depths (0-7.8 inches (0-20 cm)), although the difference in fine root depth among young (<50 years), intermediate (50-60 years), and old (>250 years) trees was not significant. Maximum depths recorded for fine roots were 16 to 20 inches (40-50 cm) [19].

Ponderosa pine is long-lived [350]; trees often reach ages of 300 to 600 years [34, 422]. On the Swauk Late-successional Reserve on the Wenatchee National Forest, Washington, age distribution of ponderosa pines ranged from 13 to 597 years, with a mean age of 110 years. Logging from the 1860s to the mid-1960s selectively removed large ponderosa pines, so old ponderosa pines are underrepresented in most stands compared to their occurrence in presettlement (before the mid-1800s) stands [106]; this is true throughout the West [168]. For the varieties covered in this review, the oldest documented ponderosa pine was 879 years old as of 2018; it grows in Newberry National Volcanic Monument, Oregon [94, 115].

Raunkiaer Life Form

Phanerophyte [448]

SEASONAL DEVELOPMENT

Ponderosa pine seed cones take 2 years to mature. First-year seed cones open for pollination soon after freezing weather stops, and pollen cones disperse pollen in spring or early summer, depending on location [422]. Seed disperses after second-year cones open in fall [523]. Seed dispersal coincides with the fire season, so seeds may disperse onto new burns soon after fire [211, 270, 530] (see Plant Response to Fire). Seeds germinate in spring. Individual needles are retained for 3 to 4 years [575], then shed in fall.

On Newman Ridge on the Lolo National Forest, Montana, seeds dispersed from early September through mid-October [494]. Table 2 shows phenological data collected over 10 years (1928-1937) in the Northern Rocky Mountains.

Table 2—Phenology of ponderosa pine in northern Idaho and western Montana, by mean date of event [484].

Event	Date
Shoot growth starts	3 May
Buds burst	11 May
Pollen dispersal starts	20 June
Pollen dispersal ends	30 June
Shoot growth stops	20 July
Winter buds form	20 July
Cones fully elongated	17 August
Cones open	5 September

In California, pollination occurs from April to June, depending on location. Cones ripen and seeds disperse in August and September [347].

Little was known of ponderosa pine's fine root phenology as of 2018. In the Central Cascades of Oregon, fine root production occurred from late May to early June, with fine root biomass peaking from late July to August [19].

REGENERATION PROCESSES

Summary: Ponderosa pine regenerates most successfully after disturbances that open the canopy and expose mineral soil. Fire is the primary agent creating these conditions. Ponderosa pine does not regenerate well in shade. Seed production varies within and among populations and between years, with dry years resulting in low seed production. Wind and wildlife disperse the seeds. Few seeds actually establish. For those that do, growth is most favorable on open sites with light shade. Low- to moderate-severity fire and/or thinning promote ponderosa pine growth.

- Pollination and Breeding System
- Seed Production
- Seed Banking
- Seed Dispersal
- Germination
- Seedling Establishment
- Plant Growth
- Vegetative Regeneration
- Mortality

Pollination and Breeding System

Ponderosa pine is primarily wind pollinated [354, 422], although some selfing occurs [514]. It is monoecious [422].

Figure 4—Second-year seed cone (left) and pollen cones (right). Terminal bud, with protective scales surrounding the tip, is in the middle. Photo used with permission of Gerald and Buff Corsi © California Academy of Sciences.

Seed Production

Ponderosa pine first produces seeds at 10 to 20 years old [347, 356]; sometimes, as early as 7 years old [422]. Seed production generally increases as trees age [356], although it may slow in very old trees [422]. Seed production varies within and among populations and across years. Generally, fewer seeds are produced in drought than in normal years. Seed predation can result in few seeds surviving to germinate and can be especially high on new burns.

Ponderosa pine tends toward masting [187, 346, 357, 389]. Within stands, large seed crops are produced every 2 to 5 years [288, 346, 347], with large, mature trees producing the most seeds [187]. Daubenmire [138] reported that in Washington, masting was positively correlated with above-average summer temperatures during the first year of seed cone development.

A review reported highly variable cone and seed production within and among ponderosa pine populations across ponderosa pine's range. Large bole diameter was the most reliable factor for predicting large cone crops, although genetics, abundant soil moisture in spring followed by soil drying in summer, nutrient-rich soils, and low rates of insect infestation and disease were also associated with high cone production. Open sites promoted fastest growth rates; in turn, this promoted highest cone production. Higher-than-average temperatures during seed cone initiation increased seed cone production, while freezing temperatures lowered production of second-year seed cones [345].

Studies in the Northern Rocky Mountains and California show variable seed production across years. On 12 sites across Idaho and eastern Washington, cone production ranged from zero to 384 cones/tree over 24 years (1958-1981) (review by [345]). On the Stanislaus National Forest, cone and seed production varied by about a factor of 2 in two different collection years [187] (table 3).

Table 3—Cone and seed production, averaged from several ponderosa pines on the Stanislaus National Forest [187].

Collection year	Cones/tree	Seeds/cone	Estimated seeds/tree
1934	100	69	1,690
1940	204	73	2,294

Seed production across 4 years on the Challenge Experimental Forest in northern California was rated "light" for 1 year, "medium" for 2 years, and "bumper" for 1 year. Across 4 years of study (1964-1967), estimated seedfall from 90- to 120-year-old ponderosa pines onto 2-acre (0.8 ha) nearby clearcuts ranged from 0 to 40,690 sound seeds/acre (0-100,545/ha). On 10-acre (4 ha) clearcuts, estimated seedfall ranged from 0 sound seeds/acre to 15,345 sound seeds/acre (0-37,915/ha) [389].

Although seed production in populations generally increases with soil moisture and decreases with stand density [345], there are exceptions. On the Deschutes National Forest near Bend, Oregon, a xeric site yielded 6 times more ponderosa pine seeds than a mesic site ($P < 0.001$). On both sites, dense stands yielded more seeds than more open stands (table 4). Cone production was positively correlated to DBH and tree height ($P = 0.05$) [328].

Table 4—Ponderosa pine stand structure and seed production over 9 months on 2 sites on the Deschutes National Forest [328].

Variable	Relatively dense, xeric site	Open, mesic site
Maximum density	80 trees/ha	18 trees/ha
Mean basal area	18 m^2/ha	4.2 m^2/ha
Mean seed production	1.7 million seeds/ha	300,000 seeds/ha

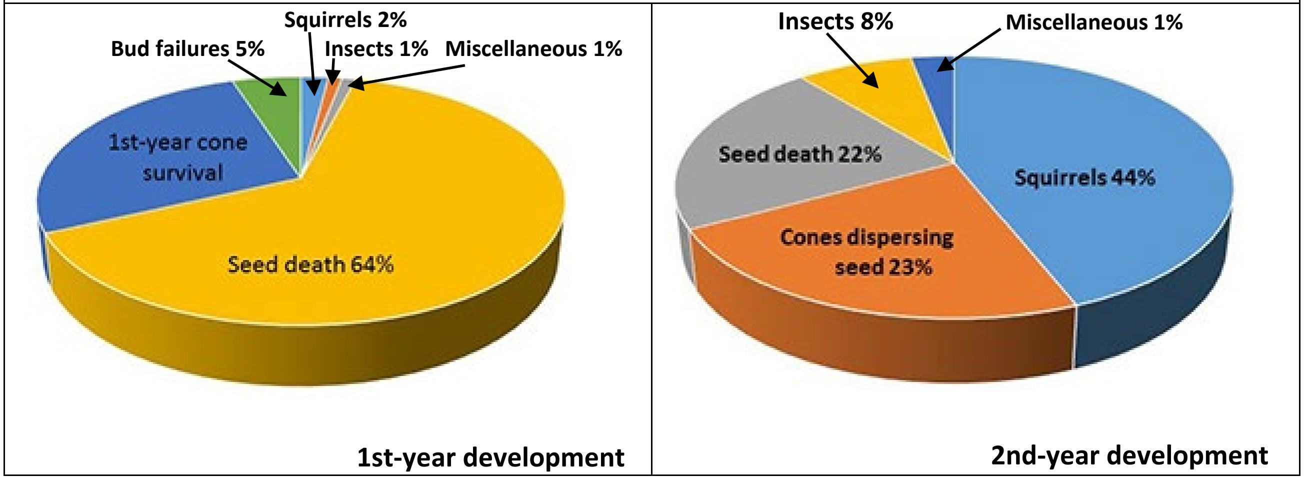
Low- to moderate-intensity fire may not affect cone production. A year after a moderate-intensity fall prescribed fire on the Coeur d' Alene Reservation, Idaho, there was no difference between ponderosa pine cone production on burned and unburned plots, and there was no difference in losses of cones to ponderosa pine cone beetles (*Conopthorus ponderosae*) on burned and unburned plots ($P < 0.05$) [293].

Many mammals, birds, and insects eat ponderosa pine seeds (see Importance to Wildlife and Livestock), and seed predation can substantially reduce ponderosa pine's crown and forest floor seed banks [279, 422, 485]. Although mineral soil favors ponderosa pine seedling establishment, seeds on mineral soil are more vulnerable to predation than seeds buried in litter or duff [279]. Several authors [398, 422] provide reviews of the impacts of seed predation on ponderosa pine reproduction.

In southern British Columbia, seed predators—mostly deer mice—removed ponderosa pine seeds from uncut and clearcut sites at high rates. A seed predation experiment revealed that after 1 week, 4% percent of hand-scattered ponderosa pine seeds remained on unprotected uncut stands, 0.4% remained on unprotected clearcuts, and 100% remained in rodent and insect exclosures [279].

A 4-year study on four sites in western Montana found few developing seeds survived to germination stage. Most cones were lost early in development. Of cones that survived to maturity, red squirrels harvested 66%. Yellow-pine chipmunks, deer mice, and birds harvested an additional 30% of seeds after seeds dispersed [485]. Seed loss is shown in figure 5.

Figure 5—Factors affecting seed loss of ponderosa pine in the 1st and 2nd years of seed development, based on data collected in western Montana [485].



Some rodent species prefer foraging for seeds on new burns. On the Lolo National Forest, Montana, deer mice were about twice as abundant in a 1-year-old burn compared to an adjacent, unburned ponderosa pine-Douglas-fir forest. Predation was about 8% higher for ponderosa pine seeds than for the smaller Douglas-fir seeds. For both species, seedling recruitment was significantly less in cages that allowed deer mouse egress than in cages that did not allow egress ($P < 0.05$ for all variables) [603]. On two sites on the Lolo National Forest, Halvorson [229] found populations of ponderosa pine seed predators—mostly deer mice and red-tailed chipmunks—increased after clearcutting and prescribed burning, likely due to easy access of ponderosa pine and other conifer seeds on the forest floor. For details, see the "Small mammals" section of FEIS's Research Project Summary of the study.

Seed Banking

Ponderosa pine has a short-term crown-stored seed bank [31, 510] and a short-term seed bank on the forest floor. Wind-dispersed seed overwinters in or on top of litter [465, 474, 493, 495]. Wildlife-cached seed may be stored in shallow soil seed banks (see Seed Dispersal). Ponderosa pine seed does not remain viable for longer than about 6 months in the field [494].

Seed Dispersal

Summary: Wind, wildlife, and people disperse ponderosa pine seed. Wildlife-dispersed seed is more likely to establish than wind-dispersed seed, although wind dispersal is more common. The winged seeds are buoyant and carry for short distances, usually no more than 150 feet (50 m) from the parent tree.

Mosaic fires that create abundant 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 [32, 151, 323, 528]. Regeneration in the centers of large burns or clearcuts is generally poor because the seed does not travel into interior portions of the burn or clearcut [32, 389]. In Oregon, ponderosa pine seed fall 120 feet (37 m) inside a clearing was only 22% of seed fall at the edge of the clearing [56].

Birds and mammals disperse ponderosa pine seeds, and dispersal distances are often greater than those achieved by wind [110]. Compared to a long-range dispersal distance of 150 feet (50 m) for wind [32], rodents may cache pine seeds over 250 feet (75 m) from parent trees [564], and Clark's nutcrackers may disperse pine seeds 1.2 to 18 miles (1.9-29 km) from parent trees [280, 546, 563]. Small mammals disperse seeds on either the soil surface or in shallow caches [110, 579]. Clark's nutcrackers disperse and bury ponderosa pine seeds in shallow caches that contain a few seeds each [355, 356, 547].

Seeds buried by rodents [329] or Clark's nutcrackers [357] have a greater chance of establishing than seeds dispersed onto the forest floor by wind. On the Deschutes National Forest, most ponderosa pine seedlings (63%-85%) that established grew in clusters attributed to natural rodent caching [330]. Ponderosa pine emergence rates on plots where seeds were buried to simulate rodent caching were more than 7 times higher than on plots where seeds were sown on top of litter or mineral soil [329].

One study suggests that seeds in small caches are more likely to establish than seeds in large caches. On the Deschutes National Forest, yellow-pine chipmunks and golden-mantled ground squirrels made small and large caches of ponderosa pine seeds, respectively. The autumn after caches were made, ponderosa pines emerged at an average rate of 17 seedlings/cache. Seventy-two seedlings emerged from the largest cache. Mortality rate of 1-year-old seedlings averaged 40%, with highest mortality in the largest caches [474].

Recaching was common in a study tracking rodent dispersal of radioactive pine seed (ponderosa pine, Jeffrey pine, and sugar pine). On the Carson Range in western Nevada, yellow-pine chipmunks practiced secondary caching or recaching as many as 3 times/cache in mast years. The level of secondary caching approximately tripled in nonmast years, with some seeds recached 5 or 6 times. Primary caches were made 3 to 266 feet (1-82 m) from parent trees; seeds were carried farther away from their parent trees in nonmast (14.9 feet (5.9 m) farther) than in mast years (15.1 feet (4.6 m) farther, $P < 0.001$). The authors concluded that masting increases dispersal efficiency and helps satiate seed predators [564].

Because it is a culturally valuable tree (see Other Uses), American Indians likely assisted ponderosa pine migration. Ponderosa pines on the Fort Leis Prairie, Washington [167], and in the Willamette Valley, Oregon [119], may have descended from plantings by American Indians.

Germination

Seeds are dormant upon dispersal, requiring stratification [50], exposure to light [243, 366], or scarification to break dormancy. A laboratory study found that breaking the seed coat (scarification) broke dormancy immediately; so did 1 to 2 months of late fall-winter stratification in a northern rough fescue grassland [50]. Viable seeds stratify naturally over winter and germinate the spring following dispersal [366, 494]. Light is not required for germination of overwintered seeds [366]. Germination is epigeal [422].

Highest germination rates occur on bare mineral soil or an ash seedbed [424, 595]. Surface fire burns away litter and prepares a mineral seedbed [1, 9, 385]. In the greenhouse, ponderosa pine seeds collected from Priest River, Idaho, showed highest mean germination (71.6%) in an ash seedbed. Germination averaged 67.2% in bare mineral soil and was least (56.7%) in duff collected beneath a mature western white pine stand [179].

Seedling Establishment

Seedlings require open areas, mineral soil, and quick access to lower soil layers for best establishment and growth [466]; thick litter and duff layers inhibit establishment [1, 5, 209, 487]. Openings larger than about 0.7 acre (0.3 ha) [306]—or overstory basal area of less than about 50 feet^2/acre (11.5 m^2/ha) [166]—are needed for substantial ponderosa pine seedling establishment. The first growing season after a fall prescribed fire in northern Idaho, mean height and basal diameter of ponderosa pine seedlings were greater on a mineral seedbed than on burned duff ($P = 0.05$) [424]. A pot study found height growth of ponderosa pine seedlings was about 50% greater in soil collected from a prescribed burn site than in soil collected from a nearby unburned site [565].

Light shade may increase ponderosa pine seedling establishment on open sites [127, 205, 327]. In central Idaho, light shade and soil scarification increased establishment in three habitat types that were either logged or burned under prescription. Moderate shrub canopy cover resulted in highest establishment of ponderosa pine seedlings in each habitat type [205] (table 5).

Table 5—Percent cover of ponderosa pine seedlings under different levels of shrub cover. Data were taken 5 or more years after thinning or prescribed fire in central Idaho [205].

Habitat type	Shrub canopy cover		
	Light (0-33%)	Moderate (33-66%)	Heavy (66-100%)
Douglas-fir/white spirea	17	42	41
Grand fir/Rocky Mountain maple	27	49	24
Grand fir/thinleaf huckleberry	28	45	27

On the Metolius Research Natural Area, density of ponderosa pine germinants and seedlings was positively associated with shrub cover, which was mostly antelope bitterbrush ($P = 0.01$). By the sapling stage, however, density of young ponderosa pines was negatively associated with antelope bitterbrush ($P = 0.0003$). At that stage, antelope bitterbrush was apparently no longer facilitating ponderosa pine growth; instead, it was becoming competitive [327].

Adequate moisture is critical for ponderosa pine seedlings, especially in their first year [5, 188, 422]. At low-elevation woodland ecotones, ponderosa pine establishment is limited by low soil moisture content in summer; at high elevations, by cold, short growing seasons [9, 422, 521]. Establishment is generally poor in dry years [510], although ponderosa pine seedlings are more drought-tolerant and hence, more likely to establish on dry sites than associated conifer species [381]. Regeneration pulses are associated with one or more consecutive wet years (review by [436]). In central Idaho, no ponderosa pine seedlings grew on clearcut plots in 1959, when summer weather was hot and dry and there was no precipitation in June. In contrast, there was "exceptional" regeneration of ponderosa pine on clearcut plots in 1963 (3,500 seedlings/acre (8,648/ha)), when summer weather was relatively cool and moist and total June precipitation was nearly 3 inches (76 mm) above normal [185].

Coarse soils can limit seedling establishment because they drain quickly. Two years after the 2002 Biscuit Fire in southwestern Oregon, overall conifer seedling establishment was greater on fine-grained soils (295-604 seedlings/acre (729-1,492/ha)) than on skeletal, coarse-grained soils (54 seedlings/acre (133/ha)) [151].

Mortality is high for germinants and seedlings [330]. Primary causes of seedling mortality include fire (see Fire Effects), drought, browsing insects and wildlife, fungi, heat, and frost [150, 186, 188, 495]. Seedlings may tolerate sustained cold winter temperatures but succumb to sudden changes in temperature, including summer frosts [167]. On Deschutes National Forest in the East Cascades, only about 3% of viable seed matured to 2-year-old seedlings. Most seedlings died soon after emergence. After 2 years, only seedlings that established beneath live cover were still alive [330].

Seedling establishment may lessen under climate change. Kemp [323] cautions that as climate continues to warm, temperature—rather than seed source—may limit ponderosa pine establishment, and "temperature may outweigh the influence of seed source availability on seedling regeneration and the post-fire environment may no longer be favorable for regeneration in much (80%) of the existing dry mixed-conifer zone". With increasing global warming, some models predict higher regeneration of ponderosa pine in the mid-2000s (2020-2059) relative to 1910 to 2014, but reduced regeneration from 2060 to 2099 as temperatures increase and soil moisture decreases [438].

Plant Growth

Summary: Ponderosa pine attains fastest growth on moist, open sites. Growth is generally slow on droughty sites such as steep, south- or west-facing slopes. Growth tends to slow in dense stands and as trees age. Prescribed fire and/or thinning promote growth.

Seedlings grow a long taproot to access lower soil layers before attaining much top growth [1, 216, 422]. One-year-old seedlings, only 2 inches (5 cm) tall, may have taproots 3 feet (1 m) long [29, 34], and 4-year-old saplings may have roots 5 feet (1.5 m) long [29]. As ponderosa pines age, they switch biomass allocation from root to shoot growth. In Lassen Volcanic National Park, California, seedlings had highest relative biomass allocation to roots and lowest biomass allocation to needle and branch growth. Saplings had highest biomass allocation to needles, and pole-sized trees had highest biomass allocation to woody tissues. Water-use efficiency increased with tree age [216].

Relatively warm winters and cool growing-season temperatures favor ponderosa pine growth, while previous-year drought impedes growth. On the Lassen National Forest, California, ponderosa pine had fastest growth rates with warmer-than-normal temperatures in January and cooler-than-normal temperatures the previous May. Higher-than-normal temperatures from September to November—and/or the previous May—slowed ponderosa pine growth rates [295]. Growing season in the mediterranean climate of southwestern Oregon and California is long and mostly limited by water availability [421].

Ponderosa pine growth is suppressed in dense stands [24, 69, 118]. In a 1947 survey on the Colville Indian Reservation in Washington, Weaver [570] compared growth and stand density in a wildfire-burned and an adjacent unburned stand. Both stands were composed of second-growth, 40-year-old ponderosa pines. By postfire year 26, trees averaged 32.2 feet (9.8 m) tall and 7.4 inches (18.8 cm) in diameter on the burned stand. They averaged 12.3 feet (3.7 m) tall and 1.7 inches (4.3 cm) in diameter on the unburned stand. Density was more than 10 times less on the burned stand (1,100 trees/acre (2,717/ha)) than on the unburned stand (14,800 trees/acre (26,556/ha)). Weaver [570] reported that "in many places the [unburned] stand is so dense as to be almost impenetrable to man or beast".

On opens sites, height growth is generally rapid in pole and early mature (early sawtimber) stages (review by [422]). Growth typically slows as mature trees age. The bole becomes wider and the crown broader, and the proportion of dead wood increases. Needle production slows with age, and tufts at the ends of branches become progressively smaller each year [9].

Low- and moderate-severity fires release ponderosa pines, encouraging postfire growth [9, 478] (see Plant Response to Fire).

Ponderosa pines of all age classes also respond well to release by thinning [55, 58, 150, 367, 411, 476]. On the Sequoia National Forest, ponderosa pines <50 years old responded to thinning with increased diameter in their lower boles. Mature trees in the subcanopy increased diameter mostly their middle boles, while ponderosa pines dominating the canopy increased diameter in mostly their upper boles ($P = 0.05$ for all variables) [26]. A 50-year study on the Blacks Mountain Experimental Forest, northeastern California, showed diameter growth of old, large ponderosa pines (>31.5 inches (80.0 cm) DBH) was greatest with 75% removal of overstory trees. Thinning ranged from 0% (control) to 95% removal. Fifty years after thinning, net volume yield of ponderosa pine stands averaged 5,350 feet^3/acre (373 m^3/ha) on 75% cut plots compared to 3,880 feet^3/acre (271 m^3/ha) on uncut plots and 5,050 feet^3/acre (353m^3/ha) on 95% cut plots. No further thinning was done in the 50 years after the initial cuts [150].

Equations to predict these components of ponderosa pine growth are available:

- diameter and cubic volume growth at various stocking levels; developed from stands in the Northern Rocky Mountains and the Southwest [155];
- height-DBH growth; curves based on site productivity and density of even-aged, 70-year old stands in western Montana [383];
- growth at three overstory densities, based on stand age; developed from stands in western Montana, Idaho, and eastern Washington [162];
- diameter growth; developed in southwestern Oregon [232]; and
- tree height based on DBH, developed for the Willamette Valley [568] and southwestern Oregon [539].

Mortality

Fire (see Fire Effects on trees) and bark beetle attacks during drought [217] are primary causes of ponderosa pine mortality. Wildfire results in high mortality of ponderosa pine across the West [422]. Windthrow usually causes localized tree death. A study across western Montana found that of 10,600 old-growth ponderosa pines, 406 died over 17 years (1948-1965). For ponderosa pines that died, 57% died from windstorms, 27% from pine beetles (*Dendroctonus* spp.), 7% from unknown causes, 6% from insects other than *Dendroctonus*, and 3% from lightning strikes. No fire-caused mortality was noted during this period of effective fire suppression [299].

Hann and Larsen [232] provide equations to predict estimates of stand mortality for ponderosa pine and associated tree species; the models were developed in southwestern Oregon. See the Fire Effects Models section for help predicting postfire mortality of ponderosa pine.

Vegetative Regeneration

Ponderosa pine does not naturally reproduce vegetatively [422].

SUCCESSIONAL STATUS

Summary: Ponderosa pine is shade intolerant. It is a successionally stable or climax species on low-elevation, dry sites and seral on more mesic and midelevation sites. At midelevations, ponderosa pine is generally seral to Douglas-fir and other more mesophytic, shade-tolerant species. It is a minor late-successional species in some poor-site (pumice) lodgepole pine stands of south-central Oregon. In southern Oregon and California, it is a late-successional species that displaces shrubs in montane chaparral. Ponderosa pine encroaches into some perennial grasslands and mountain meadows.
It establishes in canopy gaps or larger openings resulting from fire, bark beetle outbreaks, or other disturbances. Low- to moderate-severity fire maintains ponderosa pine dominance. After stand-replacing fire, succession in dry forest cover types generally follows a trajectory leading from dominance by annual herbs to dominance by conifers. Ponderosa pine is replaced successionally by shade-tolerant species with long fire-free periods, and is in decline as a forest cover type on fire-excluded sites.

Overview

Frequent, low- and moderate-severity fires favor ponderosa pine and other shade-intolerant species. Understory vegetation is top-killed or killed without much mortality of the overstory, although patches of severe fire kill the overstory and create openings that favor ponderosa pine establishment [112, 265, 504]. If fire-free intervals are long, shade-tolerant, understory Douglas-fir, grand fir, incense-cedar, and/or white fir increase in number and size, shading out ponderosa pine [24, 63, 145, 170, 182, 357]. Historically, long fire-free intervals on some sites, particularly north-facing slopes, allowed more fire-sensitive species such as Douglas-fir to develop thicker bark before the next fire, so some shade-tolerant trees survived successive fires [9].

After stand-replacement fire and/or heavy logging, succession to ponderosa pine or mixed-conifer communities generally proceeds in stages: from annuals, to perennial herbs, to shrubs, and finally to conifer dominance of the overstory [98, 529]. For example, herbs and shrubs established soon after a wildfire (1959) and salvage logging (1960) on the Eldorado National Forest, California. Prior to these disturbances, the site was a ponderosa pine-sugar pine-Douglas-fir/deer brush-manzanita/mountain misery forest. In the first 3 postfire years, annual sixweeks grasses and miner's-lettuce dominated, and pine seedlings were emerging. Blue wildrye, Lemmon's needlegrass, and California needlegrass dominated the perennial herb stage from about postfire years 4 to 8, with sprouting shrubs gaining frequency. By postfire year 8, deer brush and manzanita were more frequent than herbaceous species, but pine seedlings were overtopping the shrubs [98].

Succession generally progresses fastest on moist sites. In California, Minnich et al. [404] found density of ponderosa pine and mixed-conifer stands was positively associated with mean annual precipitation (P = 0.05). In the San Bernardino Mountains, succession from ponderosa pine to incense-cedar and white fir was more rapid on mesic than xeric sites. Across mountain ranges, successional advancement was more rapid in the Sierra Nevada than in the drier, more southerly San Bernardino Mountains. Stand densities and composition were compared from surveys conducted from 1929-1935 and in 1992 [404].

Without fire or other disturbances, riparian ponderosa pine communities are especially prone to rapid successional advancement [556]. Hardy et al. [238] report that in the interior Northwest, most riparian areas that were formerly dominated by large, open-grown ponderosa pines are now dominated by dense thickets of shade-tolerant trees, particularly grand fir.

Other than small stand-replacement and mixed-severity fires, disturbances that cause gap succession in ponderosa pine forests include western dwarf mistletoe [174], bark beetles, and various root- and stem-decay fungi [174, 496]. Western dwarf mistletoe infection on ponderosa pine tends to increase as succession advances and stand density increases [31, 57, 365, 481]. Drought can exacerbate effects of bark beetle attacks and fungal infection, accelerating succession to shade-tolerant species [496]. When shade-tolerant species are present in the understory, severe mountain pine and western pine beetle attacks may accelerate succession to shade-tolerant species rapidly. Climate change is predicted to increase attacks of pine beetles on ponderosa pine [74, 75].

Figure 6— An adult mountain pine beetle treading pitch while excavating a larval gallery in *Pinus ponderosa* var. *ponderosa*. Image by Whitney Cranshaw, Colorado State University, Bugwood.org.

Contemporary Changes in Succession

In many fire-excluded areas, ponderosa pine and other early-seral, shade-intolerant tree species have been replaced successionally by late-seral, shade-tolerant species [233, 252, 259, 364, 373, 486, 585]. Stand structure has changed from a mostly single canopy layer to multiple canopy layers [42, 268, 317, 318, 388, 404]. For example, on the western front of the Bitterroot Mountains in Montana, proportional basal area of ponderosa pine at elevations of 4,500 to 5,800 feet (1,400-1,800 m) decreased from 52% in 1900 to 26% in 1995, while that of Douglas-fir increased from 19% to 55% [252]. In the Whiskeytown National Recreation Area in the Klamath Mountains, California, relict ponderosa pines and sugar pines maintained a nearly constant annual basal growth rate of 3.7 to 4.2 inches^2 (24-27 cm^2)/tree for 50 years (1955-2005). Meanwhile, annual basal growth rate of shade-tolerant understory trees increased from 0.5 inch^2 (3 cm^2)/tree in 1955 to 2.5 inches^2 (16 cm^2)/tree in 2005. Understory species replacing ponderosa pine successionally were primarily Douglas-fir, tanoak, and white fir [364].

A study on the Stanislaus National Forest showed a trend of increasing structural homogeneity in mixed-conifer forests where fire is excluded. Comparing 1929 and 2007-2008 surveys of a mixed-conifer forest, total area in gaps decreased from 28% to 0%, while percentage of widely-spaced trees decreased from 6% to 2%. Percentage of small to medium tree patches (2-9 trees) decreased from 28% to 9%, while large tree patches (≥10 trees) increased from 66% to 89% and canopy cover increased from 45% to 62%. Percentage of shade-intolerant trees, which included ponderosa pine, sugar pine, and California black oak, decreased from 18.7% to 7.0% [373].

A study in Yosemite National Park found contemporary mixed-conifer forests are denser and have a larger proportion of late-successional, shade-tolerant conifers than historical mixed-conifer forests. On average, contemporary forests had about 3 times more trees, twice the basal area, and trees were 20% smaller in DBH than forests in the late 1890s. Historical and contemporary stand structure of the forests are compared in appendix A2 [486].

At broader scales, comparisons of aerial photos taken in the Northern Rocky Mountain, Northern Cascade, and Upper Klamath regions from 1932-1966 to those taken from 1981-1993 showed ponderosa pine forest cover types had declined across all those regions, and Douglas-fir and/or grand fir cover types had increased. However, ponderosa pine forest cover types had increased in the southern Cascades, which the authors attributed to tractor logging prior to 1932 ($P < 0.2$ for all variables) [259]. Hann et al. [233] reported that dry forests of the Northern Rocky Mountains have changed from dominance by shade-intolerant ponderosa pine to dominance by shade-tolerant Douglas-fir, grand fir, and white fir (table 6).

Table 6—Historical (1850-1900) and 1991 percent distributions of successional stages for dry forests of the Northern Rocky Mountains [233].

Successional stage	Historical (%)	1991 (%)	Change (%)
Grass/forb/shrub	18	1	-17
Early-seral (shade) intolerants	15	14	-1
Early-seral tolerant	3	3	0
Midseral intolerant	21	35	+14
Midseral tolerant	8	22	+14
Late-seral, intolerant single story	21	5	-16
Late-seral, tolerant single story	2	3	+1
Late-seral, intolerant multistory	9	8	-1
Late-seral, tolerant multistory	3	9	+6

In the Northern Rocky Mountains of Idaho and Montana, the extent of ponderosa pine and other single-storied woodlands and forests decreased by over 4 million acres (1.6 million ha) from 1900 to the late 1990s, and the extent of forests dominated by mid- to late-seral trees such as Douglas-fir increased by almost 8 million acres (3 million ha) [233]. A study in central Idaho revealed that forest density changed from 6 to 60 trees/acre (15-150/ha) in the 1850s to 250 to 600 trees/acre (620-1,500/ha) in 1993.

Mature and old-growth ponderosa pines dominated the forest in the 1850s; mature Douglas-fir dominated in 1993 [508].

Ponderosa pine may enter mountain meadows with fire exclusion, livestock grazing, or a combination. On the Lassen National Forest, it was the primary tree establishing in 10 of 11 mountain meadows sampled. Based on fire scars on trees at meadow edges, the median composite fire interval ranged from 9 to 18 years between 1750 and 1849. Fire was rare to absent on meadow edges after 1849. Ponderosa pine encroachment peaked during the late 19th century: in years when springs were cool, annual precipitation was normal, but summer precipitation was below normal. This summer-drought period coincided with unregulated, heavy domestic sheep and cattle grazing in mountain meadows, so herbaceous fuels were greatly reduced. The authors concluded that historically, wildfires controlled establishment of ponderosa pine and other conifers onto mountain meadows. Fire exclusion and intense grazing led to successional changes, with densities of ponderosa pines now high enough that type conversions from meadows to forests were occurring [416].

Gruell et al. [213, 215] provide photo-point comparisons of succession in ponderosa pine-Douglas-fir stands in Montana during the settlement period (1870s) and in 1982; these photos document increasing density in ponderosa pine stands over time. Photo points include the mouth of the Thompson River, Knowles Creek near Perman [213], the Bitterroot National Forest [215] , and a stand near Philipsburg [213]. A similar publication is available for the Boise National Forest [552]. Photo sequences from the 1950s to the 1980s document ponderosa pine entering meadows and a mountain big sagebrush community in Adams County, Idaho [548].

Gruell [214] also provides photo-point comparisons of succession in ponderosa pine-Douglas-fir stands in the Sierra Nevada during the settlement period (1849-late 1920s) and from 1992-1995; these photos document increasing stand density over time.

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 [59].

FIRE EFFECTS

Immediate (First-order) Fire Effects

- On Seeds
- On Trees
- Fire Effects Models

Fire Effects on Seeds

Crown fire or scorching kills seeds stored in ponderosa pine crowns [211]. Seeds stored in the cones of overstory ponderosa pines generally survive low- and moderate-severity surface fires [510, 529, 530, 576]. Surface fire likely kills many ponderosa pine seeds on the forest floor, although research on this was lacking as of 2018.

Figure 7—Different types of crown injury to ponderosa pine. The uppermost, green portion of the crown was unaffected by the fire. Needles in the middle crown were scorched and killed, but buds survived. Both needles and buds were killed in the lower portion [271]. U.S. Forest Service image by Sharon Hood.

Fire Effects on Trees

Summary: Crown fires kill ponderosa pines of all ages. Low-severity fire usually kills seedlings but not saplings. Mature ponderosa pines survive low- and usually moderate-severity fire. Fall fires generally cause more injury and mortality than spring fires. Old-growth (and younger) stands that have missed several fire cycles are vulnerable to fire damage or kill. Because they damage or kills roots, ground fires that burn thick duff and coarse woody debris may result in higher ponderosa pine mortality than would be expected based on aboveground injuries.

Small ponderosa pines are susceptible to fire kill [5, 178, 592]. Low-severity fire often kills seedlings, although saplings generally survive [31]. Seedlings and saplings in dense stands are more susceptible to fire injury or death than young trees in open stands [5]. 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. In a field experiment in western Montana, 16- to 32-year-old *Pinus ponderosa* var. *ponderosa* saplings survived flames applied directly to stems when stem girdling was <90% of the stem circumference. Defoliation after needle scorch had little effect on sapling mortality until >80% of needles were killed. Half of the ponderosa pines with <84% basal stem girdling were still alive in postfiring year 2. The first year of this experiment (1988) was an extreme drought year. The authors noted that partially girdled ponderosa pines that died tended to have poorer water relations (lower transpiration and stomatal conductance, and higher predawn xylem water potential) than partially girdled ponderosa pines that lived [454].

Saplings and pole-sized ponderosa pines generally survive low-severity fires unless they are growing in dense stands, which can torch [31, 178, 435, 592], and ponderosa pines over 10 to 12 feet (3-4 m) tall generally survive moderate-severity surface fires [592]. On a ponderosa pine plantation planted after a 1970 wildfire near Entiat, Washington, spring prescribed fires were conducted to reduce stocking density. Ponderosa pines were 25 to 34 years old when burning was initiated. Mortality rate was <10% for open-grown ponderosa pines and Douglas-firs that were >2 inches (5 cm) DBH. The fires mostly killed small trees (<2 inches DBH) and larger trees growing in dense patches. Within patches, ponderosa pine was more likely to survive fire than Douglas-fir [435].

Mature ponderosa pines survive low- [2, 103] and usually moderate-severity [2] fire of moderate intensity [273]. Mature ponderosa pines sometimes survive 100% crown scorch if the scale-protected buds are not killed [236, 419, 560]. Scorch damage depends on height to needles and buds from the forest floor, stand density, season of fire, and fire intensity. It is greater in dense than in open stands and generally, from summer and fall fires than from winter or spring fires [463, 540]. A scorch mortality curve is shown in figure 8.

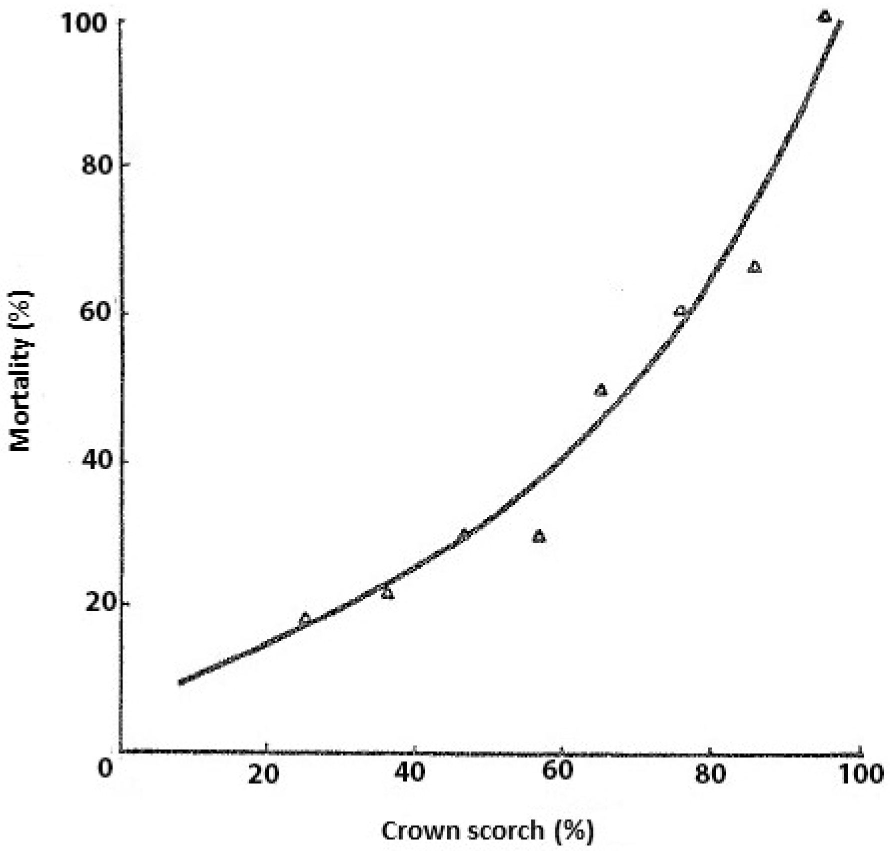


Figure 8—Mortality curve from crown scorch for mature ponderosa pines. Developed from postfire data collected on the Lolo National Forest. U.S. Forest Service image by Ryan [463].

On the Colville Indian Reservation, wildfire damage to 30- to 40-year old ponderosa pines varied from nearly 0% to 100% crown scorch. More small than large ponderosa pines died, but all ponderosa pines sustaining >95% crown scorch died. For 2-inch (5-cm) DBH ponderosa pines, 50% of those with 50% crown scorch died in postfire year 1; for 3-inch (8-cm) DBH ponderosa pines, only trees with >70% crown scorch died. For trees ≥4 inches (10 cm) DBH, only those with >80% crown scorch died. Mortality in postfire year 2 is shown in table 7 [375].

Table 7—Mean percent mortality of 30- to 40-year-old ponderosa pines (all size classes) in postfire year 2 by percent crown scorch. Based on data collected after a wildfire on the Colville Indian Reservation, Washington [375].

Crown scorch (%)	Mortality (%)
0-14	14
25-49	6
50-59	20
60-69	24
70-79	20
80-89	63
90-94	100
95-100	100

Postfire survivorship of ponderosa pine typically increases with increasing DBH (e.g., [375, 419, 486, 585]). For example, after two severe wildfires in the Sierra Nevada, ponderosa pine survivorship increased with DBH ($P < 0.01$, $n = 90$ trees). Ponderosa pines were monitored following the McNally and Manter fires on the Sequoia National Forest and the Storrie Fire on the Plumas National Forest. Fifty-one percent of trees 10 to 20 inches (25-50 cm) DBH survived, and 69% of larger trees survived [419].

However, some studies suggest that very large ponderosa pines may be more vulnerable to fire kill than midsized mature trees, especially when the larger trees sustain substantial kill in their upper crowns [273, 390, 430]. Another study on the McNally burn found that postfire mortality of mature ponderosa pines increased with increasing DBH, crown injury, and bark beetle attacks ($P < 0.0001$). A survey in postfire year 5 showed ponderosa pines >32 inches (80 cm) DBH experienced higher rates of mortality than ponderosa pines with smaller DBH. Although large ponderosa pines have thick bark and generally, high crown base heights that lessen fire damage to cambium and buds, they may also have less “vigor” and deep duff accumulations that promote ground fires [273]. Poor health can lower capacity of old ponderosa pines to recover from fire injuries [390].

Fall fires generally cause more injury and mortality than spring fires because it is usually hotter and fuels are drier in fall (e.g., [254, 463, 540, 542, 591]). For example, in four old-growth ponderosa pine stands in eastern Oregon and one in northwestern Oregon, mortality of ponderosa pines >20 inches (50 cm) DBH averaged 6.5% (6 of 92 trees) on spring-burned sites in postfire years 1 or 2, while mortality averaged 11.8% (16 of 135 trees) on fall-burned sites [591]. However, fire effects vary with ponderosa pine phenology and moisture content. Spring fire that occurs during or just after bud break can cause substantial damage to rapidly growing ponderosa pine tissues. Three years after prescribed fires on the southern Blue Mountains of southeastern Oregon, mortality of ponderosa pines >10 inches (25 cm) DBH averaged 89% on spring-burned plots, 32% on fall-burned plots, and 1% on unburned plots [540]. At Crater Lake National Park, Swezy and Agee [535] found mortality of mature (>8.7 inches (22 cm) DBH) ponderosa pines was greater after June prescribed fires (37.6%) than after September prescribed fires

(12.0%). Mortality was assessed on plots that were periodically burned from 1976 to 1986, with most mortality occurring in postfire year 1. The authors suggested that higher mortality from early-season burning may be due to differences in bud phenology and higher moisture content of ponderosa pine tissues in June compared to September [535].

Old-growth stands that have missed several fire cycles are vulnerable to fire damage or kill. An old-growth ponderosa pine-mixed-conifer stand in Glacier National Park experienced substantial mortality following the 1988 Red Bench Fire. Fire exclusion was implemented in the park in 1910, and the stand had not burned for at least 62 years. During that time, woody surface fuels built up, and Douglas-firs and western white pines established in the understory [585]. Before fire exclusion was implemented, the Blackfoot people underburned the area frequently in order to maintain the ponderosa pines, which are at the edge of their range in Glacier National Park [220, 222, 585]. Of 87 mature ponderosa pines on sixteen 0.1-acre (0.04-ha) plots, the Red Bench Fire killed 62%; 51 died immediately and 3 more died by postfire year 4. Of 33 surviving, mature ponderosa pines, 27 survived on plots where estimated flames lengths (based on scorch heights) were <2 feet (0.7 m). Nine survived and 26 died when estimated flame lengths were between 2 and 8 feet (0.6-2 m). All died in plots where estimated flame lengths were >8 feet (2 m) [585].

Ground fires that burn thick duff and coarse woody debris may result in higher ponderosa pine mortality than would be expected based on aboveground injuries [11]. Fine roots of pine trees tend to grow into duff, and smoldering fires kill fine roots [380]. Deep roots generally do not experience lethal heating [480], although old trees with large amounts of duff and litter accumulation may experience large root and/or root crown kill [271, 468]. On sites where fire has been excluded for several fire cycles (>75 years), thick, smoldering duff layers can result in long smoldering times, producing severe heating that kills roots and basal cambium [242, 314, 341, 469, 535]. Agee [11] notes that woody debris may smolder long after the flaming front has passed, resulting in death of even large ponderosa pines.

Ponderosa pines experience some die-off of fine roots during even low- to moderate-severity fires (review by [2]). This effect may not be important with low- and moderate-severity fires, because many fine roots die annually, with or without fire ([19], review by [2]). However, postfire recovery may be slow when ground fire burns into and kills a substantial number of ectomycorrhizal roots, which are often in shallow soil horizons [253]. Young and "low vigor" old-growth ponderosa pines are most likely to experience severe damage or death from fine root kill, and spring fires are more likely to damage or kill fine roots than fall fires (review by [2]).

Koonce and Roth [343] speculate that western dwarf mistletoe may alter patterns of heat transfer in infected trees, making infected ponderosa pines more susceptible to fire injury [343].

Fire Effects Models

These models 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; adapted for use across the West in FOFEM 6.0 [274];
- after fall prescribed fire using scorch height and DBH; developed for use in northern Idaho [479];
- using crown scorch and bole scorch proportions; developed for use in the East Cascades of Washington, Oregon, and California [541];
- based on percent crown volume consumed, amount of dead cambium in the bole, and presence of bark beetles; developed in northeastern Washington and southwestern Oregon [201]; and
- based on DBH and height of stem-bark char; developed in the central Sierra Nevada [449].

Based on data from 5 wildfires in California, Hood et al. [273] found crown scorch volume and crown length injury predicted postfire ponderosa pine mortality equally well. Most mortality from the wildfires (65%) occurred by postfire year 2, and ponderosa pine mortality rate had stabilized by postfire year 3 [273]. A review of methods to predict postfire ponderosa pine mortality concluded that crown scorch volume was the most effective and easiest method of predicting delayed postfire mortality of ponderosa pine [189].

Delayed (Second-order) Fire Effects

Summary: Ponderosa pine mortality may be delayed for several postfire years and may be exacerbated by drought and bark beetle attacks. Frequent, low-severity fire may increase ponderosa pine's resistance to postfire mortality from beetle attacks. Monitoring in postfire years 3 and 5 is recommended to determine delayed postfire mortality of ponderosa pine.

Postfire Bark Beetle Attacks

Scorched, live ponderosa pines are vulnerable to insect attacks, particularly from mountain pine beetles, western pine beetles, pine engraver beetles, and red turpentine beetles (review by [5]). Chances of postfire insect attacks increase with increasing fire damage (reviews by [271, 463]) and drought [189]. Attacks by mountain and western pine beetles frequently result in delayed mortality of scorched ponderosa pines [165, 271, 298]. Fifty percent or more crown scorch is associated with postfire attacks and mortality from western pine beetles (review by [5]). One year after a predominantly crown fire on the Payette National Forest, Idaho, 16.6% of ponderosa pines were still alive. In postfire year 2, only 9.5% were classified as living, and most mortality between postfire years 1 and 2 was attributed to bark beetles [124]. Perrakis and Agee [11, 430] noted that after prescribed fire in Crater Lake National Park, small (≤4 inches (10 cm DBH) and/or young (<80 years) ponderosa pines generally died in postfire year 1, while 35% of large (>20 inches (50 cm) DBH) ponderosa pines died in postfire years 3 to 7. Pine beetles (*Dendroctonus* spp.) and postfire drought were implicated in delayed deaths of the large ponderosa pines [11, 544]. Mortality from bark beetles had ceased by postfire year 4 [11].

Figure 9—A burned ponderosa pine stand in Yosemite National Park. Trees in the red and gray stages of beetle mortality survived the 2013 Rim Fire but succumbed to pine beetles by postfire years 4 or 5, which were drought years. U.S. Forest Service photo by Janet Fryer.

Delayed postfire mortality from bark beetles is not clearly related to season of burning. In Crater Lake National Park, mortality from postfire bark beetle attacks was higher after fall than after spring fires; 13% of ponderosa pines in fall-burn units died from western pine beetles compared to 6% in spring-burned units and 2% in unburned units ([535], review by [271]). Three years after prescribed fires on the Tahoe National Forest, mountain and western pine beetles killed more large ponderosa and Jeffrey pines (>20.0 inches (50.7 cm) DBH) on May-burned plots than on October-burned plots ($P > 0.055$). Across plots, western pine beetles killed 67 ponderosa pines (18.9% of total bark beetle mortality for all conifer species), and mountain pine beetles killed 56 ponderosa pines (15.8% of total) [165].

High resin flows and formation of new resin ducts increase resistance to beetle attacks in *Pinus* spp. [276, 369, 477, 566]. Studies across Utah, Montana, Idaho, and Oregon found frequent, low-severity fire induces resin duct formation in ponderosa pine, and resin duct formation declines as fires become less frequent. Ponderosa pines killed by *Dendroctonus* and *Ips* bark beetles had fewer resin ducts than ponderosa pines that survived beetle attacks ($P = 0.004$) [276].

Agee [5] reports that there is little evidence that fire injury encourages infection by pathogenic fungi. Fire scars in ponderosa pine often show little decay [5]. Typically, ponderosa pines seal catfaces off with pitch, preventing entry by fungi or insects. Four-hundred-year-old trees, scarred by multiple fires, can still remain healthy [34]. While fire-damaged roots may be susceptible to root rot fungi, there were no studies documenting this [5] as of 2018.

Postfire Regeneration Strategy

Crown residual colonizer (on site, initial community)
Initial off-site colonizer (off site, initial community)
Secondary colonizer (on- or off-site seed sources) [530]

FIRE ADAPTATIONS AND PLANT RESPONSE TO FIRE

- Fire Adaptations
- Plant Response to Fire

Fire Adaptations

Ponderosa pine is adapted to low- and moderate-severity surface fires [9]. Adaptations to fire include thick bark; a high, open crown; self- and fire-pruned branches; large, scale-protected terminal buds; high foliar moisture content; deep roots; and rapid root growth of seedlings [31, 177, 183, 463, 480]. During a fire, species with rough bark, such as ponderosa pine, likely experience lower temperatures at the bark surface than species 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 [31]. Surface fires prune lower branches, reducing chances of subsequent crown fire [29]. Buds at branch tips are protected by bud scales [31, 464] (figure 4). Trees with large buds, such as ponderosa pine, are more resistant to fire damage than trees with small buds, such as Douglas-fir [463].

Ponderosa pines of all age classes have some resistance to fire damage. Martin and Dell [386] report that even in the seedling stage, ponderosa pines in the Inland West are more fire-resistant than seedlings of associated conifer species. Ponderosa pines begin to develop insulating bark when they reach about 2 inches (5 cm) in diameter [510]; this provides enough protection to survive most low-severity surface fires [209, 510]. In the Blue Mountains, 2-inch diameter ponderosa pine saplings had 0.13- to 0.25-inch (0.33- to 0.64-cm) outer bark that protected the cambium, while the bark of white firs was thin and green at twice the diameter [224].

Figure 10—A tree “cookie” showing damage (inner fire scar, yellow arrow) sustained by a ponderosa pine when it was about 2 inches (5 cm) in diameter. U.S. Forest Service photo by Ilana Abrahamson.

Ponderosa pine is rated the second most fire-resistant species in the West, after western larch [34, 183, 308, 515, 520]. Ponderosa pine's fire resistance generally increases with size. A 2003 wildfire on the Deschutes National Forest killed most lodgepole pines, subalpine firs, and grand fir × white fir hybrids on a 500-acre (200-ha), mixed-conifer site. Large ponderosa pines had the lowest fire mortality rates among all conifers in the study area. In postfire year 1, ponderosa pines averaged 21% crown scorch and 24% bole char compared to 83% crown scorch and 65% bole char for the fir hybrids. Ponderosa pines with <60% bole scorch or maximum needle scorch heights below 55 feet (17 m) generally survived. Among size classes, 13 of 16 ponderosa pines from 7 to 15 inches (18-38 cm) DBH were still alive in postfire year 2, and 81 of 100 trees ≥21 inches (53 cm) DBH were alive. The 19 dead in the ≥21-inch DBH class were scorched high up the boles [175].

Plant Response to Fire

- Postfire Seedling Establishment and Growth
- Mature Trees
- Applicable FEIS Fire Studies

Postfire Seedling Establishment and Growth

Summary: Moderate and mixed-severity fire favors ponderosa pine establishment on new burns. Wind and wildlife disperse seeds onto burned sites. Barriers to postfire establishment include large patches of severe fire, postfire drought, interference from other conifer seedlings and shrubs, and some types of salvage logging.

Ponderosa pine establishes from wind- and wildlife-dispersed seed after fire [32, 270, 354, 530]. Much of the seed comes from on-site or nearby sources: seed that disperses from crown-stored cones soon after the fire has passed [530]. Wind-dispersed seeds typically fall within 150 feet (50 m) of the parent tree [32]. Seed dispersed by Clark's nutcrackers and small mammals can be a secondary source of postfire seedling establishment [354], 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.

Seeds disperse during the fire season, so crown-stored seeds often disperse onto new burns [31, 510]. Most seeds that dispersed onto the forest floor prior to fire—or are still in cones that get scorched or burned during crown fire—are likely killed. After the mostly stand-replacement Marble Cone wildfire in August 1977 in southern California, seeds dispersed from dead ponderosa pines in early September. The crowning wildfire apparently killed most cone-stored seeds: seeds that dispersed from the dead trees did not germinate. In postfire year 1, most viable seeds dispersed from live, unburned ponderosa pine parents 70 to 330 feet (20-100 m) away from study plots. A "large number" of ponderosa pines established in postfire year 1, but only 40% survived their first year. Seedling density slowly increased in early postfire years [211].

Establishment may be highest after moderate- or mixed-severity fires. California studies suggest that moderate-severity fire promotes postfire establishment of ponderosa pine. Four years after the 1999 Pendola Fire on the Plumas and Tahoe national forests, seedling density of ponderosa pine was highest on plots that burned at moderate severity (318 seedlings/acre (786/ha)). Seedling density was intermediate on high-severity plots (221 seedlings/acre (546/ha)) and lowest on low-severity plots (108 seedlings/acre (445/ha)). There were no ponderosa pine seedlings on unburned control plots [576]. Ten years after the Storrie Fire on the Plumas National Forest, ponderosa pine in the mixed-conifer zone had highest mean establishment on plots where fire severity was moderate (126 seedlings/acre (312/ha)).

Ponderosa pine establishment was intermediate on low-severity plots (80 seedlings/acre (198/ha)) and lowest on high-severity plots (36 seedlings/acre (88/ha)) [134].

Mixed-severity burns where fire killed the overstory provide open patches in which ponderosa pine can establish [111, 122, 145, 331]. On the Lolo National Forest of Montana, a new cohort of ponderosa pines and western larches established after a mixed-severity, mosaic fire in 1663. The fire killed all ponderosa pines on study plots, although a few western larches survived. Some stumps of remnant ponderosa pines that survived the 1663 fire—but not logging in 1919—were noted outside study plots and might have been seed sources for the 1664 cohort [42].

Establishment can be poor after large, stand-replacement fire. If open patches are too big, distance from off-site parent trees limits seed dispersal into burn interiors [32, 84, 151]. Two years after the 2002 mixed-severity Biscuit Fire in southwestern Oregon, approximately 58% of conifer seedlings in stand-replacement patches were ≤650 feet (200 m) from live conifers on the burn edge, and approximately 81% were ≤1,300 feet (400 m) away. For all conifer species present, which included ponderosa pine, mean seedling density in stand-replacement patches was >405 stems/acre (1,000/ha) within 1,300 feet of the burn edge. Seedling density dropped greatly farther from the burn edge [151]. Across the landscapes of five mixed-conifer burns in the northern Sierra Nevada, ponderosa pine and sugar pine had no seedling establishment in 72% of severely burned patches. At the plot level, 87% of severely burned plots had no pine regeneration; most regeneration was shrubs and sprouting hardwoods. Size of severely burned patches ranged from about 32 acres (13 ha) on the 1999 Lookout burn to 551 acres (223 ha) on the 2000 Storrie burn. Twelve and 33% of total area burned was stand replacement on the Lookout and Storrie burns, respectively [122].

Under favorable conditions (see Seedling Establishment), ponderosa pine seedlings establish in large numbers in early postfire years but thin over time. After spring, summer, or fall prescribed fires on clearcuts on Newman Ridge on the Lolo National Forest, density of ponderosa pine seedlings averaged 206/acre (509/ha) in postfire year 5 and 235/acre (581/ha) in postfire year 10. By postfire year 15, seedling density had decreased to 21/acre (52/ha) because some seedlings had died [494]. See the Research Project Summary of this study for further information.

Ponderosa pine's initial allocation of growth to the taproot, rather than to stems and needles, is an important trait that aids postfire regeneration. Long taproots allow seedlings to access soil moisture in lower soil profiles even on blackened and hot, burned-over soils [354].

Even so, low soil moisture is a leading cause of postfire mortality for ponderosa pine seedlings [139, 148, 444]. Following the 2002 Eyerly Fire in north-central Oregon, drought and competition with grasses for soil moisture were implicated for poor ponderosa pine establishment at low elevations. In postfire year 10, density of established (≥15 inches (38 cm) tall)) ponderosa pine seedlings increased with elevation ($P < 0.001$). No ponderosa pine seedlings had established at elevations <3,380 feet (1,030 m); greatest density of ponderosa pine seedlings was around 4,590 feet (1,400 m) Fifty-five percent of the 23,134-acre (9,362-ha)) wildfire was stand-replacing. Prior to the wildfire at low elevations, ponderosa pine was either the sole dominant or codominant with western juniper. At midelevations, ponderosa pine codominated with Douglas-fir, western larch, and other conifers. [148].

Douglas-fir, firs, and other shade-tolerant species may overwhelm the ponderosa pine seed bank if they disperse large numbers of seeds onto burned sites. Two to four years after the 1999 Pendola Fire on the Plumas and Tahoe national forests, Douglas-fir, incense-cedar, and white fir seedlings had higher seedling densities than ponderosa pine and other shade-intolerant conifers on burned sites of all fire severities. Shade-tolerant conifers dominated adjacent unburned stands both before and after fire. Therefore, shade-tolerant conifers dispersed "much higher" numbers of seeds onto adjacent burned sites compared to ponderosa pine and other shade-intolerant conifers [576].

Sprouting shrubs can interfere with postfire seedling establishment and growth of ponderosa pine [421, 451, 567]. Rejmanek et al. [451] present a growth model for ponderosa pine seedlings based on level of water competition from greenleaf manzanita. Data for the model were collected on the Blodgett Forest Research Station, California [451].

Postfire logging may slow or reduce ponderosa pine's postfire establishment. Two years after the 1992 Lone Pine Fire in south-central Oregon, ponderosa pine seedling establishment was 17% lower on sites that were salvage logged than on unlogged sites. For ponderosa pine seedlings planted on the burn, height growth was 16% less on salvage logged than unlogged sites [492]. McIver et al. [391] provide an annotated bibliography of the effects of salvage logging on ponderosa pine and other postfire conifer communities. See the Salvage logging section of this review for further information.

Mature Trees

Ponderosa pine growth tends to increase after low- and moderate-severity fires that cause little scorch damage ([353, 560, 571], review by [9]). For example, 6 years after fall prescribed fire in an open ponderosa pine/pinegrass stand on the Colville Indian Reservation, ponderosa pine diameter and height growth were greater on burned than unburned control sites ($P \leq 0.05$). Growth increases were attributed to the thinning effect of the fire, which reduced stand density from 825 to 136 stems/acre (2,038 to 336/ha) [412].

However, some stands—particularly after decades of fire exclusion—may show reduced growth after prescribed fire [499, 590] or wildfire [353] compared to prefire or unburned stands. After a September prescribed fire in another section of the Colville Indian Reservation, ponderosa pines on burned plots showed reduced height growth in postfire year 6 compared to plots in an adjacent unburned stand. This mature stand had a dense understory of shrubs and conifer saplings [590].

Effects of crown scorch: Early postfire recovery and growth rates of surviving ponderosa pines decrease with increasing crown scorch [412, 429, 533], although growth rates of scorched trees increase as needles grow completely back, which takes about 3 years [575]. 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 [465] (see Delayed Fire Effects).

When scorch damage is ≤30%, healthy, mature ponderosa pines usually recover without much slowing of prefire growth rate. Lynch [375] suggested that ponderosa pine's postfire diameter growth is reduced in the short term by 30% to 50% if crown scorch is >50%. Eight years after a wildfire on the Colville Indian Reservation, 6- to 9-inch (15-23 cm) DBH ponderosa pines with >50% crown scorch showed reduced incremental diameter growth compared to same-sized ponderosa pines with <50% crown scorch. The wildfire reached fireline intensities that far exceed those attained during prescribed burning (from 900 kW/m at night to 5,500 kW/m in the afternoon) [375].

Ponderosa pine mortality may initially be overestimated because live ponderosa pines with 100% crown scorch appear dead [480]. After the 2002 McNally Fire in Sequoia National Forest, 4-year survivorship of ponderosa pines with 100% crown scorch ($n = 354$) averaged 22% for trees 10 to 19 inches (25-49 cm) DBH, 47% for trees 20 to 30 inches (50-75 cm) DBH, and 58% for trees >30 inches DBH. DBH predicted survival rates well, with the largest trees surviving at the highest rates ($P < 0.001$). The authors cautioned that if postfire flushing of ponderosa pine buds is not taken into account, salvage logging could remove live ponderosa pines that appear dead [236]. A study in southern Oregon showed high concentrations of sapwood ethanol (≥0.3 µmol/g fresh mass) were the best predictor of 2nd-year mortality in ponderosa pines with ≥75% crown scorch [322].

Figure 11—A ponderosa pine with 100% crown scorch, just after the 2016 Roaring Lion Wildfire on the Bitterroot National Forest (left) and flushed out in postfire year 1 (right). U.S. Forest Service photos by Sharon Hood.

Fire season: Fires that occur early in the growing season may slow ponderosa pine growth if they damage tissues while carbohydrate reserves are still low [239, 535, 542]. After spring and fall fires in Colorado, Harrington [239] observed more damage to spring-burned than fall-burned ponderosa pines because the spring burns scorched new needles during bud break. However, low-severity spring fires that do not damage buds may favor ponderosa pine growth. Five years after prescribed fires in the Blue Mountains of eastern Oregon, increases in ponderosa pine basal area were slightly more on spring- than on fall-burned plots ($P = 0.10$), which the authors attributed to more soil moisture and less shrub cover on spring-burned vs. fall-burned plots [254].

In the southern Blue Mountains, growth rates of ponderosa pines were similar after thin-only, thin-and-fall-burn, or thin-and-spring-burn treatments. Researchers found that after accounting for proportion of loss from crown scorch, there were no significant differences between treatments in ponderosa pine diameter and height growth [543] (table 8).

Table 8—Changes in ponderosa pine diameter and height after thin-only, thin-and-fall (1997) burn, and thin-and-spring (1998) burn treatments in the southern Blue Mountains. Data are means (range). Differences between treatments are not significant (*P* = 0.05) [543].

Variable	Thin only (*n* = 305)	Thin-and-fall burn (*n* = 243)	Thin-and-spring burn (*n* = 304)
Diameter change 1998-2007 (cm)	2.95 (2.60-3.30)	2.97 (2.61-3.32)	2.76 (2.31-3.02)
Height change 1998-2007 (cm)	1.82 (1.50-2.14)	1.66 (1.34-1.98)	1.85 (1.53-2.17)

Postfire Resilience

Resilience in ponderosa pine ecosystems

Resilience has multiple definitions, depending on context [1]. In the context of fire disturbance, Hood et al. [272] define it thusly :
"A resilient forest ecosystem in a landscape with a historical fire regime of frequent, low-severity fire is one that can withstand disturbance and persist in a forested state dominated by shade intolerant tree species and maintain ecological processes (fire regime, hydrology, nutrient cycling, etc.). In contrast, this same landscape is not resilient if a disturbance moves the system to a new state, such as a change in species dominance or forest structure to such a degree that ecological processes are altered" [272].

It is unclear whether old-growth ponderosa pine stands that have missed several fire cycles will be resilient to wildfire. In the Bob Marshall Wilderness, Montana, at least some old-growth ponderosa pine stands withstood reintroduction of wildfire without substantial losses of large trees. Fire had been excluded from a ponderosa pine-lodgepole pine-Douglas-fir forest in the Flathead River valley for at least 70 years when the 2003 Bartlett Mountain Fire burned about 282 acres (114 ha) of the forest. Afterwards, a dense cohort of lodgepole pine and Douglas-fir established in the understory [359]. A follow-up study found that in postfire year 9, 69% of ponderosa pines >20 inches (51 cm) DBH were alive and appeared healthy, 11.5% had minor injuries, 1% had major injuries, and 18.5% were dead (*n* = 455 ponderosa pines) [363]. In 2011, the Hammer Creek Fire burned a portion of the forest that had burned in the 2003 fire. The 2011 wildfire killed the lodgepole pine and Douglas-fir seedlings and removed surface fuels. As of 2012, large-diameter (>60-inch (152-cm) DBH) ponderosa pines that survived both wildfires dominated the overstory, with large Douglas-fir codominating on some sites. The authors concluded that the second wildfire "strongly altered the successional trajectory of the study system by killing many of the lodgepole pine seedlings that established following the initial fire in 2003", restoring a "low-density mixed-conifer forest dominated by large, old ponderosa pines" [359].

Ponderosa pine also showed resilience after wildfires in close succession on the Ishi Wilderness in north-central California. Fire had been excluded from the wilderness since 1905. However, wildfires in 1990 and 1994 killed many small conifers (<14 inches (35 cm) DBH) and created gaps (0.02-0.6 acre (0.01-0.24 ha)) favorable for ponderosa pine seedling establishment. The author reported ponderosa pine seedlings were "abundant" on mineral soils in the fire-created gaps. Most (64%) ponderosa pines >16 inches (40 cm) DBH survived the wildfires [536].

Postfire recovery after a previously long period of fire exclusion will vary with site and fire history, and not all ponderosa pine communities show resilience. Stands that burn at high severity, then reburn while ponderosa pine regeneration is still young, are vulnerable to type conversions to shrubfields [120], particularly ponderosa pine forests with a thick shrub understory. On the Plumas National Forest, for example, the 2012 Chips Fire burned ponderosa pine stands that had previously burned in the 2008 Rich Fire and/or the 2000 Storrie Fire. Researchers found that time-since-initial-fire (2000 and/or 2008) and severity of the initial fire were important drivers of reburn fire severity. On reburns that had burned >9 years prior, plots that initially burned at high severity tended to reburn at high severity, and plots that initially burned at low severity tended to reburn at low severity. This relationship was not apparent in areas that had reburned ≤4 years after initial fires. Increases in shrub cover were associated with initial fire severity and time-since-initial-fire ($P \leq 0.001$ for all variables) [129].

Ponderosa pine resilience to large, stand-replacement wildfires is generally poor. In central Montana, for example, the 170,000-acre (69,000 ha) Hawk Creek Fire killed 98% of trees within its perimeter, including groves of 400-year-old ponderosa pines. By postfire year 20, few ponderosa pine seedlings had established on the burn [32].

Increasing resilience: Fire can increase resilience of large ponderosa pines by helping to restore historical stand structure and overstory composition. A review coauthored by 18 fire ecologists and foresters recommends using thinning and prescribed fire to increase resilience of dry forests by promoting development of large, old, widely spaced trees with diverse understories [265]. A study comparing drought-induced ponderosa pine mortality on sites recently burned by wildfires and on fire-excluded sites found mortality was less on recently burned sites than on fire-excluded sites. In Sequoia-Kings Canyon and Yosemite national parks, ponderosa pine plots that were burned under prescription 6 to 18 years previously had lower stem densities and ponderosa pine mortality during the third year of drought than ponderosa pine plots than had not burned since around 1870 ($P = 0.001$) [559]. Multiple entries of prescribed fire are likely needed to increase resilience of ponderosa pine forests [4, 80].

Resilience of ponderosa pine stands may decrease in the short term if severe disturbance follows thin-and-burn treatments. The Lubrecht Experimental Forest in western Montana experienced an outbreak of mountain pine beetles 5 years after fuel treatments in a ponderosa pine-Douglas-fir forest. Burn-only, thin-only, thin-and-burn, and control treatments were used. Prior to treatments, the site had not burned since the late 1800s. Both thin-only and thin-and-burn treatments restored dominance of ponderosa pine. However, after the bark beetle attacks, high ponderosa pine mortality from beetles shifted dominance to Douglas-fir in the burn-only and control treatments, but not the thin-only and thin-and-burn treatments. The authors suggested that in the short term, burn-only units were stressed beyond their ability to return to ponderosa pine-dominated stands. However, they emphasized that reintroduction of fire is crucial for long-term resilience of ponderosa pine forests, and that such stressed stands require further fuel treatments to increase their resilience [272].

Applicable FEIS Fire Studies
For more information on response of ponderosa pine to fire, see these Fire Studies:

- Research Project Summary: Vegetation response to restoration treatments in ponderosa pine-Douglas-fir forests of western Montana
- Research Project Summary: Prescribed fire and wildfire in clearcut mixed-conifer forests on Miller Creek and Newman Ridge, Montana
- Research Project Summary: Understory recovery after low- and high-intensity fires in ponderosa pine forests of northern Idaho

- Research Paper: A comparison of dry and moist fuel underburns in ponderosa pine shelterwood units in Idaho
- Research Project Summary: Changes in stand structure and composition after thinning and burning in low-elevation, dry ponderosa pine and Douglas-fir forests of northeastern Oregon
- Research Paper: Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine (central Oregon)
- Research Project Summary: Plant response to prescribed burning with varying season, weather, and fuel moisture in mixed-conifer forests of California
- Research Paper: A fuel treatment reduces potential fire severity and increases suppression efficiency in a Sierran mixed conifer forest
- Research Project Summary: Fire effects and a refined fire prescription after low-intensity spring fires in low-elevation mixed-conifer forests of Yosemite National Park, California
- Research Project Summary: Impact of summer and fall prescribed fires on fire-excluded, Sierran mixed-conifer forests in Kings Canyon National Park, California

FUELS AND FIRE REGIMES

- Fuels
- Fire Regimes

Fuels

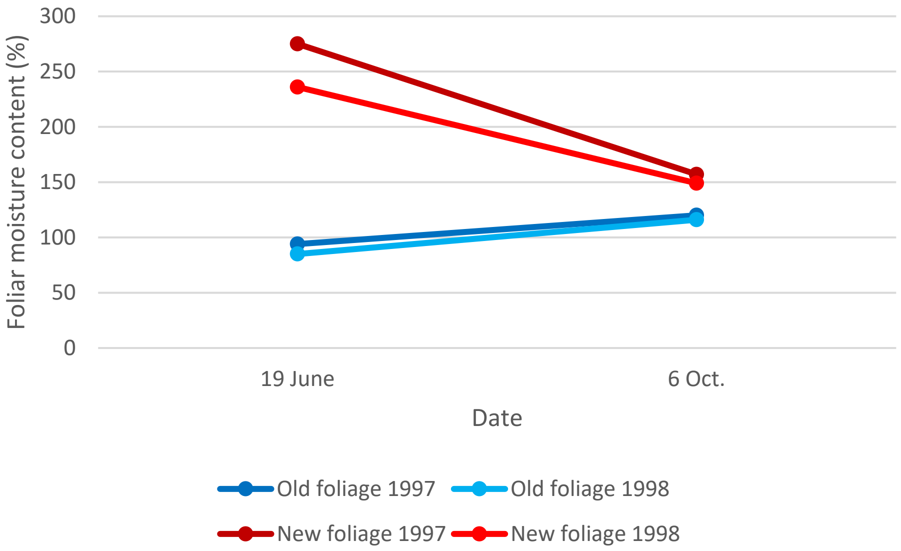
- Flammability
- Fuel Loads
- Fuels and Fire Exclusion
- Grazing
- Fuel Treatments

Flammability

Flammability of ponderosa pine trees is low due to insulative, thick bark and self- or fire-pruned branches [2]. If present, ponderosa pine's lichen load is usually light [2]. Resin accumulations [177] and infestations of western dwarf mistletoe [343] increase flammability of ponderosa pine. Ponderosa pine needle cast and other litter is highly flammable when dry [21].

Live fuel moisture of old ponderosa pine needles is generally less than that of new needles. For ponderosa pines in the Pacific Northwest and California, foliar moisture content during the fire season (July-October) ranged from 85% to 135% for old needles and from 125% to 340% for new needles (review by [326]). Moisture content of old and new needles may converge as the fire season progresses. Over 2 years in the Teanaway River valley of central Washington, foliar moisture content of new ponderosa pine needles decreased during the growing season, while that of old ponderosa pine needles increased (figure 12) [13].

Figure 12—Percent foliar moisture content of new (1 year) and old (>1 year) ponderosa pine foliage collected in the Teanaway River valley, Washington [13].



The authors concluded that risk for crown fires was highest when foliar moisture content was in the range of 100% to 120%. This occurs late in the growing season, when foliar moisture content of old and new needles are at their lowest levels [13].

Resin accumulations increase flammability of bark, and litter and duff accumulations beneath trees increase fire duration and severity [177]. Ponderosa pine needles are relatively long, so bulk density of their littler layer is relatively low [478, 517] and their flammability relatively high ([490, 491], review by [302]). A thick layer of ponderosa pine needles can ignite easily and burn completely, resulting in high soil burn severity [488].

Stands that are heavily infected with western dwarf mistletoe may be more flammable than uninfected and lightly infected stands because of increased dead crown fuels and standing dead fuels [343]. In Newberry National Volcanic Monument, ponderosa pine branches infected with western dwarf mistletoe burned for shorter periods but at higher temperatures than uninfected branches. However, infection level was a weak indicator of fine aerial and surface fuels compared to basal area or other measures of stand structure ($P \leq 0.5$ for all variables) [518].

Fuel Loads

Surface fires reoccurring several times per century historically consumed accumulated fuels on the forest floor [357]. Consequently, fires in most ponderosa pine forests were limited more by lack of fuel than high fuel moisture content [472]. Fuel loads were historically light in most areas [4, 177, 385]. Due to open stand structure and branches positioned high on boles, most fuels were surface fuels consisting of curing graminoids and/or low shrubs, scattered downed woody debris, and concentrations of litter around ponderosa pines. Agee [4] reports that many presettlement ponderosa pine communities had a “sizable” perennial herb component. Bunchgrasses make discontinuous fuels because they are widely spaced apart [581, 584], but combined with pine needles in interspaces, bunchgrasses and other herbs created flashy fuels that carried frequent surface fires [4, 9]. Where present, mountain misery often formed a continuous, flammable ground layer of fuels [82]. At the landscape level, some sites historically had relatively dense patches or understories of Douglas-fir and firs, which became ladder fuels that carried surface fires to the overstory [177].

Fuel loads in contemporary dry forests are highly variable. Within and across six ponderosa pine communities in the Rocky Mountains that ranged from southwestern Utah to northeastern Washington, canopy fuels and surface fuels of all size classes (1- to 1,000-hour) varied by a factor of 2 to 3 around the mean, with variability increasing with fuel size class [315]. In western Montana, total fuel load on the forest floor averaged 11.7 tons/acre (26.2 t/ha), with the litter load averaged 1.4 tons/acre (3.1 t/ha), (range: 0.6- 2.7 tons/acre (1.3-6.0 t/ha)) (review by [385]). Total fuel loads in ponderosa pine forests with a dense understories of shrubs and/or of pole- and small sawtimber-sized trees are high. On the Lolo National Forest, Montana, fuel load of an 80-year-old ponderosa pine/common snowberry stand with a dense understory averaged 16.5 tons/acre (37 t/ha) [490]. Brown et al. provide measurements of surface fuel loads in ponderosa pine forests of the Selway-Bitterroot Wilderness, Idaho ($n = 494$ samples) [91], and of downed woody fuel biomass in ponderosa pine stands across western Montana [92].

Rates of fuel buildup and decomposition can be used to estimate how long a fuel treatment will last and to decide which areas to treat. In dry ponderosa pine stands in northwestern Montana and central Idaho, litterfall rates averaged 0.012 pound/foot^2 (0.057 kg/m^2)/year, with little variability detected among sites. Litterfall included all fallen canopy material: foliage, twigs, small and large branches, and logs. Litterfall increased with leaf area index, basal area, and tree height ($r > 0.5$), and decay rates increased with temperature and relative humidity ($r > 0.4$) [311]. In Whittaker's Forest in Tulare County, California, litterfall biomass for ponderosa pine averaged 0.04 pound/foot^2 (0.20 kg/m^2)/year over 2 years. This was less than litterfall of associated sugar pines and white pines [12]. Fahnestock [158] provides mean biomass of ponderosa pine foliage, of ponderosa pine branchwood biomass by diameter class, and decay rates of ponderosa pine woody fuels on the Priest River Experimental Forest of Idaho, and compares those measurements to those of associated conifers. In comparisons of 5-year rates of slash decay following thinning, rates of decay for ponderosa pine slash fell between those of grand fir and western larch, which decayed fastest; and western white pine and lodgepole pine, which still had large amounts of fine fuels after 5 years on the ground. Ponderosa pine still retained most of its bark, and only 25% of twigs were decayed. Branchwood had dry rot [159].

Photo series are available for estimating fuel loads of ponderosa pine forests in western Montana [490], Idaho [410], the southern Cascades [83], and the northern Sierra Nevada [83, 490].

Models to predict ponderosa pine fuels are available to:

- predict weight of slash, including ponderosa pine needles, branches, bole tips, and boles; developed for use throughout the West [93];
- estimate crown weight [90] and density [89, 90]; developed for use in the Northern Rocky Mountains;
- assess risk of crown fire; developed from ponderosa pine stands in western Montana [489];
- predict bark-to-weight volume and weight ratios of ponderosa pine logging slash; developed for use in Idaho, Washington, and Oregon [512];
- estimate crown width; developed in western Oregon [231];
- predict weight of logging and thinning residue, including ponderosa pine needles, branches, bole tips, and boles; developed for use on the west slope of the Cascades [511];

- estimate total aboveground biomass and bole biomass of young (<11.5 ft (3.5 m) tall) ponderosa pines in south-central Oregon [460];
- estimate crown volume and width; developed in the Sierra Nevada [79]; and
- predict fuel deposition rates (foliage, bark and crown fragments, cones, and woody debris) for four stem size classes, based on stem and crown characteristics; developed in the Sierra Nevada [562].

Fuels and Fire Exclusion

Advancing succession under fire exclusion has resulted in buildup of live and dead fuels in ponderosa pine communities [432, 434, 572, 573] as shade-tolerant species replace ponderosa pine (see Successional Status). For example, in the interior Columbia River Basin, fires in communities with mostly low-severity fire regimes (<26-year fire intervals) were more common in 1900 than in the late 1990s (23% of all 1-km^2 pixels mapped to that fire regime in 1900 vs. 13% in 1990s). The authors noted that fire regimes have changed more in dry forests and woodlands than in mesic forests [409]. Longer fire intervals mean dead fuels have more time to accumulate and live fuels more time to grow. Many contemporary ponderosa pine forests have denser stand structure than historical stands [4, 170, 181, 209, 317, 340, 365, 409]. For example, Fitzgerald [181] reports that stand densities of several ponderosa pine communities in central Oregon have increased from 20 to 50 trees/acre (49-124/ha) in the 1910s to 500 to 1,000 trees/acre (1,235-2,470/ha) in the 2000s. Shade-tolerant seedlings and saplings in the understory create ladder fuels that increase fuel continuity. Late-seral conifers such as firs tend to have higher leaf areas than early-seral species such as ponderosa pine, resulting in increased crown fuel loads. Also, the branches of fir and other late-seral conifers tend to be more evenly distributed along the length of their boles. This results in increased *vertical* fuel continuity compared to stands dominated by ponderosa pines with fire-pruned branches. In late succession, crowns of shade-tolerant species are often dense and continuous, creating *horizontal* continuity in crown fuels (review by [318]).

Grazing

Livestock grazing reduces fine fuel abundance and continuity in ponderosa pine communities [73, 461, 534]. Woody fuels tend to increase because grazing promotes conifer seedlings and saplings at the expense of palatable herbaceous species. In central Washington, a site that had never been grazed or logged had an open stand of ponderosa pines with a “luxuriantly thick” layer of grass. Shrubs and conifer seedlings were sparse. A nearby site that had been continuously grazed for 40 years but never logged had a sparse herbaceous layer but around 3,000 ponderosa pine, Douglas-fir, and western larch seedlings/acre (8,000/ha). In the Bitterroot Mountains of Idaho, ponderosa pine stands in a cattle exclosure had half as many conifer seedlings and saplings (trees <2 inches (5 cm) DBH) as stands outside the exclosure. As grazed stands aged, Douglas-firs were successionally replacing ponderosa pines, and grazed stands had more woody fuels than the exclosed stand [73]. In in a ponderosa pine/antelope bitterbrush community in the area, plots grazed by cattle from spring through fall had more young ponderosa pines (0.2- to 8-inch (5-20 cm) diameter) than ungrazed exclosure plots (22.5 vs. 224.8 trees/acre (55.6 vs. 555.6/ha), respectively). Cover and frequency of palatable grasses were lower in grazed than ungrazed plots ($P < 0.05$ for all variables) [602].

Fuel Treatments

Treatments that reduce surface, ladder, and crown fuels—such as thinning and prescribed fire—may reduce fire severity and potential for crown fire [35, 38, 81, 173, 181, 471, 525]. For example, understory thinning or single-tree selection followed by prescribed fire reduced density and basal area of mixed-conifer forests in the southern Cascades and Sierra Nevada for at least 8 to 15 years compared to untreated stands ($P < 0.05$) [113]. A review concluded that both prescribed fire and mechanical fire surrogate treatments are generally successful in reducing fuels in the short term, so treated stands are more resilient to wildfires. The authors cautioned that because treatment effects are transient, repeated fuel-reduction treatments are needed [525]. See Fire Management Considerations for details on using prescribed fire in ponderosa pine stands.

Fire Regimes

- Background
- Fire Regimes by Region
- Patterns in Fire Regime Characteristics across Regions

Background: Historically (mid-1850s- 1900s), fire maintained ponderosa pine as a community dominant throughout its range (e.g., [28, 35, 38, 81, 173, 193, 310, 471]). In 1902, Leiberg [362] called fire the "most potent factor in shaping the forest" in the northern Sierra Nevada. "The general character of the forest, the relative ratio of different species composing it, the density and capacity in mill timber of the different stands, litter undergrowth, etc., in fact almost every phase of its condition, has been determined by the element of fire" [362]. A 1914 publication described fire behavior and effects in ponderosa pine forests of the East Cascades of Oregon thusly: "In the pure yellow-pine forest, fire runs on the ground surface, scarring the bases of a few trees, eating out the butt and felling an occasional tree, and killing all the seedlings and some of the saplings" [413].

Primary factors influencing fire behavior in ponderosa pine forests include fuel loads and stand structure; topography and other site characteristics; and fire weather [67, 310, 472]. Interactions of these factors result in topographical, elevational, and local differences in fire regimes. Ponderosa pine communities on some sites historically experienced mostly surface fires, and on some sites they experienced larger proportions of mixed-severity fires, with localized severe surface and crown fires. Proportion of mixed-severity fire tends to increase with slope and elevation [237, 310, 471]. Where mixed-severity fires predominated, patch sizes were highly variable [120, 310].

Fires were apparently widespread in presettlement ponderosa pine forests, with many acres burning annually [67, 107, 524]. For example, Barrett et al. [67] estimate that 5% of ponderosa pine cover types in the Inland Northwest burned annually prior to 1900: over 1.2 million acres (490,000 ha) of 24 million acres (9.7 million ha) (review by [67]). Similarly, before 1860, about 5.5% of ponderosa pine communities in Sequoia-Kings Canyon National Park burned annually (~2,822 acres (4,142 ha)/year over 40,939 acres (16,568 ha)) (review by [107]).

Fire Regimes by Region

FEIS provides several region-level publications that describe historical fire regimes and contemporary changes in plant communities in which *Pinus ponderosa* var. *benthamiana* and/or *P. p.* var. *ponderosa* were historically dominant:

- Fire regimes of Northern Rocky Mountain ponderosa pine communities
- Fire regimes of ponderosa pine and montane mixed-conifer forests of the East Cascades
- Fire regimes of conifer forests in the Blue Mountains
- Fire regimes of montane riparian communities in California and southwestern Oregon
- Fire regimes of California mixed-conifer communities: Information from the Pacific Southwest Research Station and LANDFIRE

For information on other plant communities in which these varieties of ponderosa pine occur, enter “ponderosa pine” in the FEIS home page under "Find Fire Regimes".

Patterns in Fire Regime Characteristics across Regions

- Fire frequency and type
- Fire severity
- Ignition
- Fire season
- Fire size and pattern
- Changing fire regimes

Fire frequency and type

Summary: Before European settlement around the mid-1850s, low-elevation dry ponderosa pine and dry ponderosa pine-Douglas-fir forests had mostly frequent, low- to moderate-severity surface fires, although small patches of high-severity surface fires and crown fires were common. Ponderosa pine forests historically had the shortest fire intervals of any forest type in the West. Fire frequency and severity generally increase with slope and decrease with elevation. Fire frequency in riparian ponderosa pine areas was sometimes longer than but often similar to fire frequency in upland ponderosa pine areas. Paleo studies show that fire frequency in dry mixed-conifer forests has varied with climate warming and cooling throughout the Holocene.

Historically, fire intervals were similar across the ranges of *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa.* They averaged about 10 years and ranged from 1 to 80 years (e.g., [31, 225, 268, 387, 472, 554], reviews by [196, 302, 303]). In the Northern Rocky Mountains, fire intervals in the presettlement period (late 1800s-early 1900s) ranged from 6 years to 31 years, with intervals from 6 to 13 years reported most often (reviews by [196, 209]). For example, Arno [28, 30] reported mean fire intervals of 6 to 11 years (range: 2- 20 years) for ponderosa pine/Idaho fescue habitat types (1680-1910) on three sites in the Bitterroot Mountains of Montana. He noted that there may have been shorter fire intervals that were undetected due to lack of fire scars [30]. Mesic stands, which usually had a larger component of other conifer species, historically had a larger proportion of mixed-severity fires [209], with longer fire intervals [43]. In Douglas-fir habitat types where ponderosa pine is the seral dominant, mean fire intervals in the Northern Rocky Mountains historically ranged from 6 to 50 years ([1, 64, 65, 522], reviews by [196, 510]). In the Blue Mountains of Washington and Oregon, presettlement fire intervals ranged from 10 to 49 years (review by [302]). On the east slope of the Cascades, they ranged from 5 to 25 years with a mean of 13 years ([157, 513], reviews by [10, 303]). In California, they ranged from 11 to 16 years, with mean minimum fire intervals of 5 years and mean maximum fire intervals of 40 to 80 years ([107, 554], review by [472]).

Modeling projects that fire intervals averaging <25 years allow ponderosa pine to maintain dominance over its more shade-tolerant conifer associates [313]. Ponderosa pine stands on very xeric sites were historically able to perpetuate without frequent fire [385].

Historical fire intervals tended to be longer in the northern than in southern portions of *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa*’s ranges. However, the differences were not great, and long intervals between fires were uncommon. For the Stein Valley of British Columbia, where ponderosa pine is at its northern limits, the mean fire interval was 21 years in Douglas-fir-ponderosa pine forests (period: 1700-1900) [268]. For the San Bernardino Mountains of southern California, where ponderosa pine is at its southern limits, the mean fire interval was 10 years in dry conifer forests (period: 1797-1905) [387].

Burning by American Indians increased fire frequency near villages and camps [23, 60, 66, 109, 203, 582, 586]. Many low-elevation, mixed-conifer communities had shorter mean fire intervals than would be expected based on lightning ignitions alone [22, 23, 60, 66, 203]. For example, natural ignitions alone do not account for the very frequent fires that occurred in some ponderosa pine-California black oak communities of the Sierra Nevada [22, 23, 203].

Differences in topography result in local differences in fire frequency and severity. Generally, fires are more frequent on warm, south- and west-facing slopes and low slopes than on cool north- and east-facing slopes and upper slopes [61, 104, 267, 459]. In the Stein Valley of British Columbia, for example, fire intervals in mixed-conifer stands averaged 14 years on south-facing slopes and 24 years on north-facing slopes ($P = 0.05$, time frame 1750-1950) [267]. In the Klamath Mountains of northwestern California, presettlement (1740-1949) fire intervals averaged 5.9 years on southwest and west-facing slopes, which were vegetated with old-growth Douglas-fir-ponderosa pine stands. Fire intervals averaged 13.1 years on all other slopes, which were vegetated with mostly pure, old-growth Douglas-fir stands [537]. In mixed-conifer stands in the Klamath-Siskiyou region of Oregon and California, fire severity was positively correlated with south aspects and negatively correlated with large DBH ($P \leq 0.01$ for all variables). Data were collected from the 2001 Quartz Fire burn in southwestern Oregon and the 1999 Big Bar Complex burn in northwestern California [15].

Fire frequency does not vary among aspects on all sites, however [472]. On the Dinkey Creek Watershed in the Sierra National Forest, mean fire intervals for ponderosa pine-white fir and other forest types in the mixed-conifer zone (4,800-6,400 feet (1,450-1,950 m)) ranged from 3.19 to 5.44 years (time frame: 1771-1873) Differences between plots, aspect, elevation, and slope were not significant [440]. Mean fire intervals were also similar on two sites on the east slope of the Cascades, Washington (time frames for the 2 sites: 1700-1860 and 1750-1860). On north-facing slopes, they averaged 6.8 and 8.1 years. On south-facing slopes, they averaged 7.1 and 6.1 years [157].

Fire intervals in ponderosa pine forests generally increase with elevation [2, 61, 104, 267, 459, 473, 513] due to a shorter growing season, more snowfall, less fuel accumulation, and moister fuels early in the fire season at higher elevations [473]. In a broad-scale metaanalysis, increasing elevation was positively correlated with lengthening mean fire intervals across the Black Hills, Northern Rocky Mountain, Blue Mountain, and the East Cascade regions ($P < 0.05$) [392]. At Crater Lake National Park, for example, plots in low-elevation ponderosa pine/snowbrush ceanothus had mean point fire intervals of ≤15 years, while plots in a higher-elevation ponderosa pine-white fir/pipsissewa/sidebells wintergreen plot had a mean point fire interval of 28 years (time frame: 1748-1902) [394]. Other studies document historical fire intervals of ponderosa pine communities increasing with elevation in the East Cascades in Oregon ([572], review by [5]) and California ([108], reviews by [472, 554]).

Historically, fire frequency and severity were highly variable in riparian ponderosa pine communities [500, 501], with fire frequencies differing by region, forest type, topography, and fire history [153, 423, 500, 501, 555, 556]. Riparian communities can burn at high severity during drought or with high winds [120]. However, many riparian ponderosa pine communities apparently burned at low severities but less frequently than upland ponderosa pine communities [120]: from 2 to 5 times per century [40, 238, 388]. Other riparian ponderosa pine communities burned about as frequently as upland communities [423]. While Skinner [501] found median fire intervals in the Klamath Mountains were twice as long in riparian Douglas-fir-ponderosa pine zones than adjacent uplands, Olson [423] found mean fire intervals were similar in riparian and upland ponderosa pine-Douglas-fir forests in the Blue Mountains of southern Oregon. A study on the Lassen National Forest found that prior to fire exclusion in the early 1900s, stand structure, fuels, and fire intervals were similar in riparian and upland mixed-conifer forests ($P < 0.05$ for all variables). However, a comparison of contemporary and reconstructed historical conditions found riparian forests have become significantly more fire-prone (denser, with higher fuel loads) in contemporary times [555, 556].

Paleo studies show that fire frequency in dry mixed-conifer forests tends to increase with climate warming and decrease with climate cooling [71, 441, 583]. However, determining Paleolithic fire regimes of ponderosa pine and other dry-site forests is difficult because dry forests with frequent fires tend to produce indiscreet charcoal peaks. Lake sediment core studies suggest summer-dry regions of the Northern Rocky Mountains exhibited highest fire activity during the Early Holocene (11,000-7,000 BP; generally warm, dry climate) and the Medieval Warm Period (~1,000 years BP; warm, dry climate). Drought conditions during those times were more severe than in the 20th Century [583]. Lake sediment core studies in the Lake Tahoe Basin found fire episodes were relatively infrequent in dry mixed-conifer forests during the late-glacial Early Holocene (14,000-11,000 BP; generally cool, moist climate); peaked during the xerothermic Middle Holocene (10,000-4,000 BP; warm, dry climate); then generally decreased through the Late Holocene (4,000-0 BP; generally cool and dry climate), but with increased fire episodes during the Medieval Warm Period (1,000-800 BP). Fire episode frequency in the early 2000s was at one of the lowest points in at least the previous 14,000 years ([71], review by [472]).

Fire severity

Summary: Low-elevation dry ponderosa pine and ponderosa pine-Douglas-fir forests historically had mostly low- and moderate-severity fires, with high-severity fire occurring in small patches. Fire intensity was historically low on most sites. Across ponderosa pine's distribution, fire severity varies with stand structure and elevation.

Historically, low-elevation, dry ponderosa pine and ponderosa pine-Douglas-fir forests had mostly low- and moderate-severity fires ([4, 9, 237, 260, 268, 278, 310, 333, 371], reviews by [196, 302]), although high-severity fire occurred in patches ([51, 237, 260, 264, 278, 310], reviews by [196, 302]). Syntheses of fire history studies across several regions indicate that low- and moderate-severity fires dominated ponderosa pine communities in the Northern Rocky Mountains [196], Blue Mountains [302], East Cascades [303], and California [472]. Fire intensity was historically low on most sites (flame lengths of <2 feet (0.6 m)) [51], although flare-ups in patches of shrubs and young conifers were historically common and remain so today [195].

Even at low elevations, ponderosa pine forests historically contained some stands of moderate to dense structure that burned at moderate to high severities [47, 237], suggesting a mixed-severity regime at the landscape level. Historically, ponderosa pine stands sometimes experienced severe surface or crown fires, even on sites where fire was usually of low to moderate severity. This likely occurred when fire intervals were longer than usual, so litter and understory fuels built up, or when fire weather was severe [5]. In the Pacific Northwest and northern California, for example, low-severity fire historically predominated on most ponderosa pine forest sites, but some sites also experienced mixed-severity fires [517]. Safford et al. [472] reported that In the Sierra Nevada, ponderosa pine and Jeffrey pine forests "in their reference state were extremely heterogeneous, and were characterized by areas of low-, moderate-, and high-severity fire (but with the balance more shifted to low severity than is currently the case)". Although low- and moderate-severity fire still dominate contemporary ponderosa pine landscapes, the proportion of fires that burn at high severity has increased [472].

In addition to low-severity fires, moderate-, mixed- [15, 52, 120, 282, 420, 510], and high-severity [52, 120, 282, 420] fires are important in shaping ponderosa pine forests [39, 43, 52, 282, 420]. Arno et al. [39] described mixed-severity fires and fire regimes thusly: "Characteristically, a mixed-severity fire regime will have a number of individual fires that burn at mixed severities. It may also have some stand-replacement fires and some nonlethal fires. Individual mixed-severity fires typically leave a patchy, erratic pattern of mortality on the landscape, which fosters development of highly diverse communities". Large fires are typically a mix of low to high severity [51]. Based on aerial photographs taken in the 1920s and 1930s, subwatersheds (10,000-40,000 acres (4,000-20,000 ha)) of ponderosa pine-Douglas-fir communities in interior British Columbia experienced about an equal mix of low- and high-severity or stand-initiating fire (~22% each), and about 55% mixed-severity fire [263].

Fire severity [310, 513] and the proportion of stand-replacement fire tends to increase with elevation ([392, 431, 473], reviews by [196, 302]). Soeriaatmadja [513] speculates that while moister conditions in high-elevation ponderosa pine sites (4,200-4,600 feet (1,300-1,400 m)) decrease fire *frequency* compared to lower-elevation sites, the higher densities of high-elevation forests increase fire *severity* and the chances of crowning when fires do occur.

Fire severity in contemporary riparian ponderosa pine communities is similar to that of upland ponderosa pine communities on some sites. For the 2002 Biscuit and 2003 Bear Butte and Booth Complex wildfires in western Oregon, fire severity in ponderosa pine riparian zones was strongly associated with and similar to fire severity in adjacent upland zones. There were no significant differences in percent crown scorch and basal area mortality between riparian and adjacent upland plots, although char height and percent exposed mineral soil were less in riparian than in adjacent upland zones ($P < 0.01$) [227]. In the Butte and Booth Complex Fire, basal area mortality was higher in the ponderosa pine community than in riparian mixed-conifer or dry mixed-conifer communities, but percent exposed mineral soil was lower ($P < 0.05$) [228].

Across ponderosa pine's distribution, patch sizes of severe fire are becoming larger in contemporary dry forests compared to patch sizes of severe fire in presettlement dry forests ([144, 198, 401, 504, 580], reviews by [196, 303]). Some claim that fire sizes are considerably larger than in the past [504], although fire history studies suggest that large fires occurred in presettlement times (see Fire Size and Pattern).

Ignition

Lightning was the primary source of ignition in presettlement ponderosa pine forests [6, 28, 68]. American Indians intentionally set fires in some ponderosa pine stands, especially near villages and camps. At least locally, this maintained open ponderosa pine forests [66, 402]. The Kalapuya, for example, conducted regular burning—possibly annually—to maintain ponderosa pine-Oregon white oak woodlands in Willamette Valley [119]. However, the extent of historical burning by American Indians is largely unknown [402].

Fire season

Across the ranges of *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa*, the fire season historically ran from late June to September or October. Most fires occurred from midsummer to early fall [43, 337, 472, 486, 506, 524, 538].

Limited studies suggest that growing-season fires increase with decreasing latitude. For mixed-conifer forests, the number of fires that occurred during the growing season increased from the southern Cascades to the southern Sierra Nevada. For example, a mixed-conifer site on the Lassen National Forest had mostly dormant-season (late fall-very early spring) fire, with 5% middle earlywood, 5% latewood, and 90% dormant fire scars. A mixed-conifer site on Mountain Home State Forest (south of Sequoia National Park) had mostly late-season fire, with more fires beginning earlier in the growing season (1% middle earlywood, 16% late earlywood, 61% latewood, and 20% dormant fire scars) compared to the Lassen site (review by [524]).

In mixed-conifer forests on the North Coast Ranges of California, Skinner et al. [503] found that relatively mesic sites historically (1700-1900) burned in late fall. In this region, earlywood scars result from spring and early summer fires; latewood scars from mid- to late summer fires; ring boundary scars from late summer or fall fires [503]; and dormant scars from late fall or winter fires [524]. Most fire scars were located in latewood or at latewood boundaries (23% in latewood and 68% at ring boundaries). On very dry, low-elevation sites near the Sacramento Valley, however, most fire scars occurred in earlywood (88% in earlywood and 15% at ring boundaries) [503].

Fire size and pattern

Fires in ponderosa pine ecosystems were historically “quite diverse in size and shape”. Both small and large fires were common, but large patches of severe fire were uncommon (review by [312]). Patches of severe fire were generally larger in mixed stands than in ponderosa pine stands [121, 312]. A review found mostly heterogeneous, mosaic spatial patterns for reference-condition pine and mixed-conifer forests. The mosaics consisted of 1) openings, 2) widely-spaced single trees, and 3) dense patches of trees, with adjacent or interlocking crowns. Most often, the dense patches were <1 acre (0.4 ha) but sometimes up 10 acres (4 ha). Large open patches were most common in stands that experienced both low- and moderate-severity fires. Only studies of presettlement stands or relict stands with intact fire regimes were reviewed; the scope of the review included studies across the western United States [359].

Precise fire sizes in presettlement ponderosa pine communities are unknown, but limited evidence suggests that most fires were <10,000 acres (4,000 ha). Studies in the Cascade Range found both small and large fire sizes, with fires of mostly low severity. A fire history study in the East Cascades of Oregon suggests that fires in dry ponderosa pine forests were likely of moderate size and frequent. Two sites separated by 6 miles (10 km) had 32 different fires between 1778 and 1900, but only two fires were cross-dated to the same year on both sites. Most fires did not scar all trees in 40-acre (16-ha) plots [85], so fires were either small, scattered, or of such low severity that many trees were not scarred [5]. An analysis of past fires in the East Cascade and Selkirk ranges of eastern Washington found fire sizes in four study areas ranged from 740 to 22,000 acres (300-9,000 ha), with a mean of 6,800 acres (2,460 ha). The study used GIS and fire scar data to estimate burning patterns from 1700 to 1850; study areas ranged from 96 to 38,815 acres (4,033-15,708 ha). Fires extended beyond study boundaries, so these fire sizes apply only to the study areas [325].

A study in Yosemite National Park found that before 1899 (year of the last widespread wildfire in the study area), median fire size was 285 acres (115 ha) across 5,250 acres (2,125-ha) of mixed-conifer forests. The forest was mostly multiaged, but small patches (<0.5 acres (0.2 ha)) of similarly-aged trees suggest that high-severity fire created small forest openings [486].

Large, unburned patches are often left within burn perimeters ([282, 482], review by [196]) For example, from 1984 to 2010 in Yosemite National Park, wildfires in ponderosa pine stands burned in a patchwork of fire severities and left large, unburned patches within burn perimeters. Lidar scans showed 62% of a 2,691-acre (1,089-ha) ponderosa pine forest burned. Within burn perimeters, most patches were of either low severity (40% of burned area; 655 acres (265 ha)) or moderate severity (30%; 495 acres (200 ha)) [31]. Smaller areas within the burn perimeter (20%; 320 acres (130 ha)) [31] scanned as “Landsat-undifferentiated patches” (i.e., unburned islands [306, 342] and high-severity patches (9%; 150 acres (62 ha)) [31].

Figure 13—The 2016 Roaring Lion Wildfire on the Bitterroot National Forest was of mixed severity, producing a mosaic of burn severities across a ponderosa pine and mixed-conifer forest landscape. U.S. Forest Service photo by Janet Fryer.

Large fires are not historically unprecedented [577]. Barrett et al. [67] stated that “large fires were common on most historical western US landscapes and they will continue to be common today”. In the Northern Rocky Mountains, there were at least 35 large fire episodes that burned dry forests between 1540 and 1940, at a mean interval of 20 years in ponderosa pine stands [67]. In southern California, the 273,300-acre (110,600-ha) Cedar Fire was widely viewed as an anomalous event resulting from past management practices and drought. It burned ponderosa and mixed-pine stands in October 2003 and was the largest in 100 years of record keeping [312]. However, Keeley and Zedler (unpublished data cited in [312]) report that a wildfire in September 1889 burned approximately 308,900 acres (125,000 ha) of similar vegetation in the same region [312]. Keane et al. [312] contend that rather than an anomalous event, the Cedar Fire is best viewed as a 100-year event; however, they note that in ponderosa pine stands, most large fires were historically nonlethal surface fires of mixed severity, while contemporary fires such as the Cedar Fire have larger components of stand-replacement fire.

Although large fires are relatively rare in contemporary forests (1%-2% of all starts) compared to all fires, they account for most of total area burned. In the 2000s, large fires accounted for about 95% of total area burned across the West. Much of the area burned was ponderosa pine and other dry forest types [587]. In Sequoia National Forest, the 16,875-acre (6,829-ha) Manter Fire and the 47,899-acre (19,384-ha) McNally Fire accounted for two-thirds of the total area burned from 1950 to 2005 [419].

Changing fire regimes

Over millennia, a wide range of conditions (stand structures, species composition, disturbance regimes) have occurred in dry-forest types. Although no period of time can be determined as the “correct” reference period, fire histories of the 500 years preceding European settlement can provide reference points from which to compare contemporary fire regimes in dry-forest ecosystems [43]. Compared to presettlement dry forests, contemporary dry forests are experiencing reduced ecosystem function; have longer fire intervals; and relatively less low-severity fire and more high-severity fire. Safford et al. [472] report that the "role of fire has changed from one of forest maintenance (of relatively open-canopy, low-fuel-accumulation conditions with dominance primarily by fire-tolerant species) to one of forest transformation, where dense stands of fire-intolerant species and heavy fuel accumulations are more likely to burn at high severity, resulting in major ecosystem changes". In the northern and middle Sierra Nevada, mean percentage of fire-interval departure from historical reference condition was 85% to 100%, with fire intervals at least 3 times longer in the early 2000s than in presettlement times (review by [472]). In chronosequence studies of ponderosa pine-Douglas-fir forests on the Lolo and Bitterroot national forests, western Montana, basal area of Douglas-fir ($P = 0.027$), total shrub cover ($P = 0.032$), forest floor thickness ($P = 0.006$), and phenols extracted from the forest floor ($P = 0.003$) increased with time-since-fire, while available soil nitrogen decreased ($P < 0.07$). The authors suggested that phenolic compounds accumulating in the soil may be affecting nitrogen transformations, making soil nitrogen less available to plants. Time-since-fire ranged from 2 to 132 years [377].

Fire intervals in ponderosa pine communities have lengthened greatly since the 1930s, when fire exclusion became effective. This has resulted in denser stand structure, increased fuel loads, and changes in plant species composition in the Northern Rocky ([41, 42, 221, 320], review by [196]) and Blue ([7, 395], review by [302]) mountains, the Pacific Northwest [7, 245, 458], and California ([149, 191, 472], review by [472]). For example, Arno et al. [42] report that on the Lolo National Forest, the estimated mean fire interval in ponderosa pine forests in the 1990s was three times the pre-1900 mean (84 vs. 28 years), and the longest fire interval was two times the pre-1900 maximum (88 vs. 44 years). The authors found that stand basal area had about doubled (e.g., 176 ft^2/acre in 1991 vs. 85 ft^2/acre in 1900 (40^2/ha vs. 20 m^2/ha)), with basal area of Douglas-fir 10 times as great in 1994 than before 1900 [42].

Range of departure from presettlement fire regimes is high in dry, low-elevation forests of the West. Analyses of the range of departure from historical fire regimes in the southern Cascades and Sierra Nevada found that modern low- and midelevation forests are "overwhelmingly" experiencing less low- and moderate-severity fire than what occurred in presettlement times. Range of departure was based upon BioPhysical Setting succession models of yellow pine (ponderosa pine and Jeffrey pine), dry mixed-conifer, and moist mixed-conifer forests. For yellow pine, mean area that burned annually at low and moderate severities was 8 times less in modern (1984-2009) than in presettlement times (before 1850) [379]. Analyses of dry forests across the northern Great Basin, the Interior Columbia Basin, and the upper Klamath Basin found that forests in which large, shade-intolerant species such as ponderosa pine had been harvested had the greatest range of departure from historical stand structure and community composition of all forest types, which the authors attributed to fire exclusion and past logging [446].

The proportion of high-severity fire that burns over ponderosa pine landscapes is increasing [114, 121, 265, 312] (see Climate change). Descriptions of burn sizes in Forest Service reports from the early 1900s suggest that large patches of high-severity fire were historically uncommon in dry and mixed-conifer forests of the Sierra Nevada. Succession modeling also suggests that widespread fires with large stand-replacement patches were uncommon in presettlement ponderosa pine forests [402]. Using Monitoring Trends and Burn Severity (MTBS) maps of mixed-conifer forests in northwestern California, Miller et al. [400] found that for large fires (>990 acres (400 ha)), the total proportion of area that burned at high severity increased from 1984 to 2004. Using satellite imagery of ponderosa pine and mixed-conifer forests of eastern California and western Nevada, they found a similar trend for fires ≥200 acres (80 ha), with the proportion of fires burning at high severity increasing from 1984 to 2010 ($P < 0.05$) [399, 403].

Climate change: Resilience of ponderosa pine forests is declining under warming temperatures and low soil water availability. Reduced snowpack, earlier springs, summer drought, warmer temperatures year-round, and severe bark beetle outbreaks have resulted in increased tree mortality throughout the West [74, 265, 437, 470]. Effects of climate change in ponderosa pine forests are exacerbated by fire exclusion [8, 470] and past timber harvesting that selected for large ponderosa pines [8].

Changing climate may result in elevational distribution shifts of ponderosa pine. A warmer, drier climate may favor ponderosa pine on formerly mesic sites that are becoming drier [72, 126, 316, 545], and ponderosa pine may be displaced on some dry sites that are becoming even drier [126, 545]. In southwestern Oregon, ponderosa pine series are predicted to replace white fir series on some sites. On the lower east slope of the southern Cascades, ponderosa pine may be replaced by big sagebrush steppe [192]. However, Haugo et al. [255] suggest that at big sagebrush steppe-ponderosa pine ecotones, fire exclusion is a more important driver of successional dynamics than climate.

Increases in the proportion of area that burned at high severity in ponderosa pine forests across the West have been attributed to climate change and fire exclusion [452, 523, 545, 588]. Analyses of climate change and associated fire trends across Yosemite National Park (747,988 acres (302,700 ha)) showed a significant decrease in depth and duration of snowpack, beginning in the mid-1980s (figure 14, $P = 0.02$), with an attendant increase in acreage burned. Annual area burned averaged 2,100 acres (850 ha)/year from 1962-1983, but it averaged 8,229 acres (3,330 ha)/year from 1984-2005. The proportion of the landscape that burned at high severity increased significantly ($R^2 = 0.39$. $P = 0.001$), and the authors predicted further increases an annual area burned with continued climate warming. Natural ignition sources increased with drought. From 1984-2005, more lightning strikes occurred in dry than in normal or wet years ($P < 0.001$). Forecasts for 2020-2049 include decreased snowpack, a 10% increase in lightning strikes, 19% increase in ignitions, and a 22% increase in area burned at high severity compared to 1984-2005 [371].

- Higher air and ground temperature
- Lower fuel moisture (drier or drier longer)

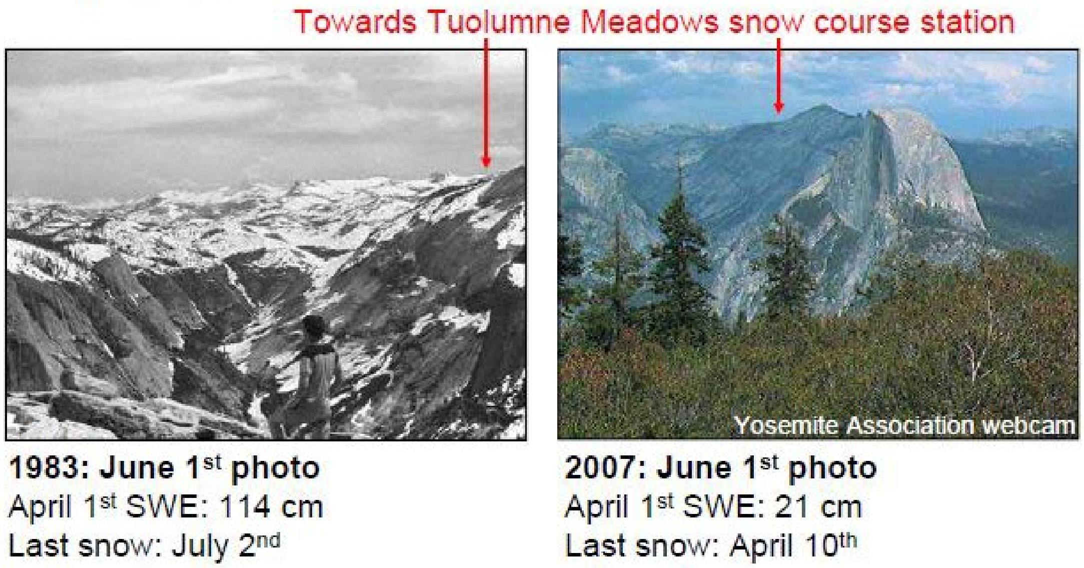


Figure 14-Changes in landscape flammability in Yosemite National Park. National Park Service image from Lutz et al. [371].

FIRE MANAGEMENT CONSIDERATIONS

- Using Fire
- Dwarf Mistletoe
- Bark Beetles
- Snags
- Wildlife
- Nonnative Plants and Fire
- Surrogate Fire Studies

Using Fire

- Objectives for Using Fire
- Wildland Fire Use for Resource Benefit
- Prescribed Fire

Objectives for Using Fire

Frequent low- to moderate-severity surface fires reduce fuel loads and kill young conifers in the understory; reduce chances of mortality of mature ponderosa pine from subsequent fires; help restore reference-condition forest structure and composition; promote regeneration of shade-intolerant conifers; and increase resilience of dry forest ecosystems [3, 246, 250, 260, 598]. Agee [3] estimated that a fire that burns 1,438 acres (582 ha) of an eastside ponderosa pine forest in the Cascade Range of Washington every 15 years consumes an average of 22 tons/acre (50 t/ha) of biomass.

Managing for healthy, sustainable ponderosa pine stands requires defining desired stand conditions, objectives to be met for attaining those conditions, and the most effective tools (ecological, economic, and social) for achieving the objectives [43]. Objectives for prescribed fire in ponderosa pine stands include [114, 170, 240, 241, 265, 574]:

- reducing high fuels loads to reduce the potential for severe wildfire;
- reducing high numbers of conifer seedlings and saplings;
- reducing thickness of the organic soil layer, exposing at least some mineral soil as a seedbed; and
- restoring historical stand structure and plant community composition (see Increasing resilience).

In stands that have missed several fire cycles, prefire thinning is often recommended to reduce fire severity and mortality of large ponderosa pines (e.g., [35, 37, 38, 102, 197, 250, 284, 455]). Fiedler et al. [170] recommend selective or partial cutting prior to prescribed fire to:

- remove sapling and pole trees;
- manipulate species composition to favor ponderosa pine; and
- reduce overstory density.

Retaining large, old trees is important for wildlife habitat (see Old Growth and Snags for Wildlife), retaining high-quality seed sources, and preserving age and size class diversity. Projects that target small and medium-sized trees for harvest are most likely to reduce fire hazard because density of trees in those size classes is usually greatest [143] and as ladder fuels, small and medium-sized trees increase the potential for crown fire [38, 102, 265].

Wildland Fire Use for Resource Benefit

Because they reduce fuel loads, wildland fires can act as fuel treatments that reduce the size, severity, spread, and frequency of subsequent fires. Parks (cited in [125]) stated “In the western U.S., prescribed burns are typically only a couple hundred acres or less—they barely make a dent. Wildland fires cover a lot more ground and have a lot more treatment impact”. In dry forests, wildfires tend to reduce the severity of subsequent fires for up to 18 years; however, this effect diminishes under severe fire weather [125]. Parks emphasized that “Suppressing a fire can be a lost opportunity to restore ecological resilience, especially during non-extreme weather conditions” (cited in [125]).

In dry forest types, allowing wildfires to spread into older burns when fire weather conditions are moderate can limit fire spread and lessen chances of stand-replacement fire [425, 527]. For example, in warm, dry, low-elevation forest types in wilderness areas of western Montana and northern Idaho (Crown of the Continent Ecosystem, Selway-Bitterroot Wilderness, and Frank Church-River of No Return Wilderness), fires ≥50 acres (20 ha) limited spread of subsequent fire. However, this effect ceased around postfire year 6 [425].

Prescribed Fire

Summary: Prescribed burning can be conducted under limited conditions, when fuel moisture and weather conditions favor safely reducing surface and ladder fuels and conifer densities. Fires must be timed when moisture content of duff is low enough for most duff to be consumed. Fall burning is often recommended to reduce fuels, except in areas with heavy fuel loads. Repeated thin-and-burn treatments are recommended to restore historical stand structure; follow-up treatments are needed to maintain stand structure. Raking beneath old ponderosa pines prior to burning may help protect the old trees from fire damage or kill.

- Season
- Thinning and burning
- Raking
- Salvage logging

Season

Prescribed burning for fuel reduction is often best accomplished in fall. Due to high fuel moisture content [304], severity of spring prescribed fire may so low that fuel reduction objectives are not met [250]. On the Priest River Experimental Forest and the Payette National Forest in Idaho, duff reduction from prescribed fires in Douglas-fir-ponderosa pine stands was <10% on moist plots burned on 1 June (88%-91% moisture content of duff) but ≥90% on dry plots burned on 13 and 14 September (35%-41% moisture content of duff). Woody fuel reduction was <30% on moist plots but as much as 70% on dry plots. Shelterwood cuts were done prior to burning. See the Fire Study by Simmerman et al. [498] for the shelterwood and fire prescriptions and further details on study results. At Crater Lake National Park, late spring-early summer prescribed fires (20-28 June) in a mixed-conifer forest reduced surface fuels by 37% compared to prefire fuel load, while fall prescribed fires (9-10 October) reduced total fuels by 75%. In postfire year 1, reduction of fine fuels was greater with fall fire than with late spring-early summer fire, although fine fuel loads on late spring-early summer burns were less than on unburned controls ($P < 0.0001$) [430]. On the Lick Creek Experimental Forest in Montana, Harrington [241] found soil heating and damage to overstory ponderosa pines was minimized and consumption of fine and small woody fuels optimized during prescribed burning when duff moisture averaged 50%, fine fuel moisture 9%, and large woody fuel moisture 90%.

In areas with high fuel loads, early-season burning may create patchy, mosaic fires more safely than fall fires. In a mixed-conifer forest in Sequoia National Park, prescribed burning on 20 and 27 June—about 6 weeks after snowmelt—resulted in a patchwork of fine-scale heterogeneity in stand structure [338, 339]. Knapp and Keeley [338] suggested that patchiness created by the early-season fire was similar to the patchiness of historical fires that burned in summer and early fall, when fuels were drier but fuel loads were less.

Thinning and burning

Many researchers report that most ponderosa pine forests in late succession cannot be restored with prescribed fire alone [5, 80, 102, 169, 173]. On the Lubrecht Experimental Forest, for example, thin-and-burn treatments reduced stand density, canopy cover, and potential for torching and crown fire most effectively. Thin-only treatments were rated “intermediate” in effectiveness, while burn-only treatments were least effective [173]. Fielder et al. [169] stated that restoration is “complicated by profound changes in stand composition and structure, poor tree vigor, and fuel accumulation”. Burning unthinned stands where ponderosa pine is already stressed may result in high ponderosa pine mortality. Restoration will usually require thinning prior to prescribed fire. Thinning prescriptions are available for mixed-conifer forests in the Sierra Nevada [336] and ponderosa pine stands of various structure (second-growth, even-aged; densely stocked, uneven-aged; and densely stocked, old-growth) in the Northern Rocky Mountains [169].

A metaanalysis of ponderosa pine restoration studies across ponderosa pine's distributional range found strong indication that thin-and-burn treatments reduced stand density and surface fuels more effectively than thin-only, burn-only, or no treatment. Researchers found no significant difference in effectiveness of thin-and-burn treatments across regions, although they acknowledged that most restoration studies (85%) included in their analyses had been conducted in California and the Southwest [197].

A model suggests that in the long term, heavy thinning from below—followed soon after by prescribed fire and follow-up thin-and-burn treatments at least every 30 years—reduces woody fuels, stand basal area, and fire hazard; and increases yield of merchantable timber more than light thinning followed by the same treatments ($P = 0.05$). The model used data from ponderosa pine and Douglas-fir stands across Montana [54].

Repeated treatments will usually be required to restore historical stand structure on sites that have had nearly a century of fire exclusion and fuel accumulation and have missed several fire cycles [5] (e.g., see the Research Project Summary by Metlen et al. [396, 597]). Agee [5] asserts that "attempts to complete the restoration in a single fire are not realistic". The first-entry fire is best conducted under "very moist" conditions, followed by fires in successively drier conditions [5, 80]. Where understory sprouting shrubs such as ceanothus are dense, two fires in short succession are recommended. The first fire top-kills shrubs and stimulates germination of shrub seeds. The second fire, timed about 3 years later, reduces density of sprouting shrubs and kills shrub seedlings [384, 567]. On the Blacks Mountain Research Natural Area on the Lassen National Forest, a single, low-severity prescribed fire reduced litter, 10-hour fuels, and killed some small understory trees in a Jeffrey pine-ponderosa pine forest. Simulations predicted that fire hazard would be "quite high" within 4 to 6 postfire years due to small, dead trees and litter accumulation, and that it would take as many as three applications of prescribed fire to achieve fuel and fire hazard reductions achieved by one application of mechanical treatment followed by prescribed fire [502].

Once treatments have reduced stand density, periodic follow-up treatments are required to maintain open ponderosa pine stands [246]. For example, thinning and prescribed fire treatments on the Okanogan-Wenatchee National Forest killed all grand fir and Douglas-fir seedlings and saplings from the understory of study plots in a ponderosa pine forest. By postfire year 9, however, seedling densities averaged 51/acre (125/ha) for Douglas-fir and 289/acre (713/ha) for grand fir [246]. Studies on the Lick Creek Demonstration Forest in western Montana found that tree biomass on thin-and-burn units recovered to levels on control units by postfire year 13, although thin-and-burn units still had lower forest floor biomass than control treatments in postfire year 20 ($P = 0.05$). A review reports that in dry forests, prescribed fire generally requires reapplication about every 8 to 10 years to reduce accumulation of dead fuels and prevent establishment of shade-tolerant conifers [117, 553]. Duration of treatment effectiveness will vary with region, climate, soils, and other factors that affect site productivity [210].

The benefits of thinning followed by prescribed fire have been documented in studies conducted in north-central Washington [442], the Blue Mountains [597], southern Oregon [430, 491], and northern California [180, 374, 457, 471, 505, 526]. Two such examples, from Oregon and California, follow.

In the Blue Mountains of northeastern Oregon, both thinning alone and burning alone modified stand structure and tree species composition slightly in closed-canopy *Pinus ponderosa* var. *ponderosa* stands in the stem exclusion stage, while a combination of thinning and burning had greater effects. Stands were dominated by large (≥21 inches (53 cm) in diameter), 70- to 100-year-old ponderosa pines, with smaller, understory ponderosa pines and Rocky Mountain Douglas-firs that had regenerated after extensive partial cuttings. Thinning selectively removed 4- to 10-inch (10-25 cm) diameter ponderosa pines and Douglas-firs, while burning killed many small-diameter Douglas-firs and most Douglas-fir seedlings. Thin-and-burn treatments resulted in greatest reduction in conifer seedling density and basal area of overstory conifers, reaching the targeted goal of 70 feet^2/acre (16.0 m^2/ha). The authors suggested that repeated treatments were needed in 10 to 15 years to bring stand structure and composition more in line with historical conditions. They commented that one set of treatments is not likely to mitigate nearly 80 years of fire exclusion and fuel accumulation in low-elevation, dry forests [597]. For further information on the effects of thinning and burning treatments on ponderosa pine and 48 other species, see the Research Project Summary of this study.

On the Plumas National Forest, fuel treatments in 2006 reduced fire severity in ponderosa pine stands during the 2007 Antelope Complex Fire, and crown fires tended to transition to moderate- or low-intensity surface fires when burning into treated areas (figure 15). Less than 20% of areas that were either masticated or burned under prescription the year prior burned severely, while 45% of untreated areas burned severely ($P < 0.0001$). However, some treated areas burned at high intensity, especially during the first 2 days of the fire, when fire weather was most severe [180].

Photos: Fire Behavior Assessment Team

Figure 15—Low- (left), moderate- (right), and high-intensity fire resulted as the Antelope Complex Fire moved through areas that had been burned under prescription the previous year [180]. U.S. Forest Service photos.

Similar studies documenting lower severity of wildfires on sites previously treated with prescribed fire are available for ponderosa pine-Douglas-fir stands on the Lick Creek Demonstration Site of the Bitterroot National Forest [36], the Lolo National Forest of Montana [160], the Payette National Forest [27], the Okanogan-Wenatchee National Forest near Wenatchee, Washington [245], the Stanislaus National Forest [372, 374], and the North Coast Ranges of California [408]. However, similar to the Antelope Complex Fire [180], restoration treatments may not reduce fire severity or area burned during extreme fire weather [204, 372].

For literature providing a range of options and prescriptions for thinning, mechanical treatment to reduce fuels in ponderosa pine and other dry forests of the western United States, see these sources: [289, 297].

Raking

Raking large accumulations of duff away from old, legacy ponderosa pines prior to burning may help protect them from fire damage [271, 275]. Duff is generally drier and more flammable in fall than in spring, so raking before fall prescribed fire is more critical [271]. A study in central Oregon found raking around ponderosa pine boles prior to fall prescribed fire reduced bole cambium damage compared to unraked boles ($P = 0.05$). Raking before spring prescribed fire, when duff was more moist, had no significant effect [443]. Hood et al. [275] found it took an average of 16 minutes/person/tree to rake around large ponderosa pines in the Sierra Nevada.

However, raking before prescribed fire has had variable effectiveness in protecting large ponderosa pines, depending on soil type, fine root density, and time-since-raking [535]. Kolb et al. [341] provide a review of rake-and-burn studies conducted to help protect legacy ponderosa pines from fire damage.

Salvage logging

Salvage logging is controversial due to potentially detrimental effects on postfire stand structure [76, 101, 143, 433]; native understory species [300, 433]; wildlife [101, 269, 283, 433] (see Cover Value); and soils and hydrology [1, 101, 433]. The effects of postfire logging depend on fire severity; intensity and timing of the logging; and other management activities [433]. This FEIS review does not comprehensively review the scientific literature on effects of salvage logging, but Burton and Franklin [101] and Peterson et al. [433] provide reviews of the effects of salvage logging on postfire ponderosa pine communities. Burton and Franklin [100] provide guidelines for reducing the impacts of salvage logging.

To ensure large, live ponderosa pines are not harvested, managers may elect to postpone salvage logging for at least 1 postfire year. Mature ponderosa pines may survive 100% crown scorch, as long as the scale-protected buds are not killed [236, 419, 560] (see Fire Effects on Trees).

Leaving some snags is generally recommended when burned areas are salvage logged [76, 143]. Some recommend leaving at least 50% of snags in all diameter classes and leaving all snags and living trees >150 years old [76, 143]. In western Idaho, the half-life of ponderosa pine snags was longer on unlogged burns (9-10 years) than on salvage-logged burns (7-8 years). This was mostly because snags were smaller on salvage-logged burns; therefore, they fell sooner [462].

Dwarf Mistletoe

Prescribed fire may reduce incidence of western dwarf mistletoe in infected stands [262]. An eastern Washington study found fall prescribed fire reduced western dwarf mistletoe infection on ponderosa pine more than spring prescribed fire ($P \leq 0.10$). On all plots, treatment effects diminished after 20 years

[262]. In an unthinned ponderosa pine stand central Oregon, moderate-intensity spring prescribed fires (15 and 25 May) scorch-pruned many infected branches; they also reduced surface fuel loads and understory cover. Stands with severely infected trees tended to be dense, and fire was severe in these dense stands. These patches had greatest mortality from fire, reducing the overall proportion of infected trees in the stand. In a thinned stand, fall prescribed fire—which burned at moderate intensity and scorched the dwarf mistletoe—was more effective at reducing western dwarf mistletoe than spring prescribed fire, which burned at low intensity and did not cause much dwarf mistletoe scorch because flames were too low. Additionally, fall fires killed much of the current-year western dwarf mistletoe seed crop. The authors concluded that low-intensity fires are insufficient to reduce western dwarf mistletoe infection; scorch heights of 30% to 60% of live crown height are needed to reduce infection rates to “tolerant levels” [343].

Bark Beetles

The combination of increasing stand density under fire exclusion, warming temperatures, and severe bark beetle outbreaks has resulted in high ponderosa pine mortality on many sites [74, 163]. Across the West in the early 21st century, bark beetles caused higher rates of ponderosa pine mortality than wildfire [74, 137].

With drought and climate warming, risk of bark beetle attacks is high in low-elevation ponderosa pine communities [74, 163, 368]. Modeling predicts that by the end of the century, the most favorable thermal habitats for mountain pine beetles will be at the lowest- and highest-elevation forest types. At low elevations and with warming temperatures, mountain pine beetles can produce two generations per year. Bentz et al. [74] predict that across the Northern Rocky Mountains, pines growing at low elevations will be subject to more mountain pine beetles outbreaks than pines growing at midelevations.

Bark beetle populations may increase after thin-only treatments, while thin-and burn treatments may help reduce incidence of bark beetle attacks [272, 442]. On the Tahoe National Forest, activity of red turpentine beetles was higher in plots that were thinned and chipped (attacks on 19% of residual stems) and in plots that were thinned, chipped, and raked (12%) than in plots where fuels were lopped and scattered (3.5%) or left untreated (4%) ($P < 0.05$). The authors concluded that chipping may result in unacceptable levels of ponderosa pine mortality due to beetle attacks [164]. On the Okanogan-Wenatchee National Forest, thin-only and thin-and-burn treatments were enacted 10 years before the 2006 Tripod Complex Fires. The wildfires burned into treated and untreated control units. In postfire year 3, probability of bark beetle (*Dendroctonus* and *Ips* spp.) attacks on ponderosa pines increased with DBH and was highest in thin-only units, moderate in control units, and lowest in thin-and-burn units ($P = 0.05$). For example, probability of attack for ponderosa pines 32 inches (80 cm) DBH was approximately 50% on thin-only, 25% on control, and 15% on thin-and-burn units [442]. See Increasing resilience for further information on bark beetles and thinning.

Snags

Snags provide wildlife habitat and contribute to soil development and productivity. Land managers are required to retain some snags for wildlife when enacting management activities [116]. A management guideline for the Forest Service’s Northern Region reports that ponderosa pine snags “are considerably more important for wildlife” than Douglas-fir or lodgepole pine snags. They remain upright longer, decay in a manner favorable to cavity nesters, and are more available at elevations preferred by most mammals and nesting birds [99]. In southern Oregon and northern California, the half-life of ponderosa pine snags was between 3 and 10 years [321, 352]. About 7% of ponderosa pine snags fell each year

[352]. On the Lolo National Forest, Montana, ponderosa pine age before death was positively associated with snag longevity, with snags standing 10 years after death averaging >225 years old at time of tree death ($P < 0.05$) [509].

Although it creates new snags, fire also tends to accelerate decay and fall of existing snags. Some ponderosa pine snags remain upright for more than a century [9]. Snags with fire scars tend to remain upright longer than snags without fire scars because fire-scarred trees produced more resin at their bases while alive [167]. On the Lassen National Forest, ponderosa pine and Jeffrey pine snags lost their crowns and shed their bark faster on plots burned under prescription in June or September than snags in adjacent unburned plots. In postfire year 7, 57% of snags on burned plots had lost "large portions" of their crowns, while only 29% of snags on unburned plots lost large portions of their crowns. Fifty-seven percent of burned snags had also lost >10% of their bark, while snags on unburned plots lost <10% of their bark. The author cautioned that snag retention in forests with a natural fire regime may be different, and that further studies are needed to better understand the relationships between fire, tree decay, and snag fall rate [360]. Compared to prefire falldown rates, overall snag fall rate increased after prescribed fire in mixed-conifer sites in southern Oregon and northern California, although fall rate by species was not determined [352]. A study on the Pringle Falls Experimental Forest, Oregon, found that 10 years after a wildfire, about half of ponderosa pines killed by the fire had fallen (117 of 212 snags). In postfire year 22, about 78% of fire-killed ponderosa pines (165 snags) had fallen [136]. A similar study in a mixed-conifer forest on the Sierra National Forest found snag loss was greater after an initial prescribed fire compared to losses after a second prescribed fire. Snag losses were partially offset by snag gains from fire mortality. Net loss on study plots was 0.7 snag/acre (1.7/ha, 34%) after the initial application of prescribed fire, and <0.4 snag/acre (1/ha, 15%) on unburned control plots and on plots burned 6 or 7 years after the initial prescribed fire. Since nesting birds prefer large ponderosa pine snags, the authors recommended protecting large snags from damage by prescribed fire [49].

Wildlife

Different wildlife guilds and species prefer different stages of postfire succession. Maintaining the full range of postfire habitats helps ensure a diversity of animal species (see Importance to Wildlife and Livestock).

When conducting prescribed burns, leaving patches of late-successional trees can retain "habitat islands" for wildlife requiring late-successional forest habitats (e.g., spotted owls and fishers). A review states that likelihood of active crown fire in habitat islands may be lowered by buffering the islands with areas that have been thinned from below. However, the authors caution that how such buffers affect quality of late-successional habitats is unknown [265].

Large wildfires that occur after many decades of fire exclusion reduce habitat for many wildlife species, including those favoring old growth. For example, analysis of California mixed-conifer forests on the Eldorado National Forest found that the 2014 King Fire, which burned 97,720 acres (39,545 ha), greatly reduced habitat of California spotted owls. On severely burned sites, the probability of California spotted owl extirpation or site abandonment was about seven times higher after the fire (88%) than before the fire (12%), and the owls had the greatest annual population decline observed over 23 years. The wildfire rendered large areas of forest unsuitable for California owl foraging in postfire year 1 [301].

Nonnative Plants and Fire

Because disturbance and opening the canopy favors many invasive species, cover of nonnative, invasive species may invade or increase in numbers after fire [46]. However, relatively few studies to date (2018) documented large postfire increases in cover of nonnative invasive species in *Pinus ponderosa* var.

benthamiana or *P. p.* var. *ponderosa* communities. In a review, Johnson et al. [296] noted that most studies of postfire establishment of nonnative species in ponderosa pine communities were conducted in Arizona, and are likely not applicable to ponderosa pine communities in more northerly regions. Regional differences in postfire responses of nonnative species can be expected, given the wide distributional range of ponderosa pine. Further, studies of nonnative species that establish in ponderosa pine communities after fire are largely short term (usually 1-5 years), so information on the long-term persistence of nonnative species is sparse [296].

Abundance of invasives may be higher in ponderosa pine stands that are treated with thinning and burning compared to untreated stands; however, invasives may not have serious ecological impacts if their postfire cover is low. Studies in California suggest that impacts of invasive species on ponderosa pine ecosystems are not as great as in nearby ecosystems such as sagebrush, and fire regimes of ponderosa pine and mixed-conifer ecosystems have not changed due to invasives [335]. On the Lubrecht Experimental Forest, cover and richness of invasive herbs in ponderosa pine stands were higher on thin-only and thin-and-burn plots compared to burn-only and control plots, with greatest increases on thin-and-burn plots ($P = 0.05$). Stands were thinned in winter over snowpack and burned the next May or June. In postfire years 1 and 3, cover of five invasives (bull thistle, Canada thistle, common mullein, houndstongue, and musk thistle) was high enough on treated plots that they were considered indicator species of those treatments [147]. Maximum cover (peaking 1-4 years after fire) of invasive species never reached 2.5%, and cover of nonnative invasives had decreased by postfire year 14 [135].

Cheatgrass and other nonnative annual grasses can increase continuity of fine surface fuels and promote fire spread (e.g., [37, 140, 319, 393]); however, as of 2018 studies did not document large increases in cheatgrass cover after fire in *Pinus ponderosa* var. *benthamiana* and *P. p.* var. *ponderosa* communities. In the Northern Rocky Mountains, cheatgrass often forms dense rings around individual ponderosa pines after fire, but generally does not spread farther [219]. In Kings Canyon National Park, summer or fall prescribed fires had no effect on cheatgrass cover compared to unburned control plots ($P > 0.05$) [319]. On the Eldorado National Forest, however, cheatgrass established in a Sierran mixed-conifer forest after the 1992 Cleveland Fire. In 2001, the St. Pauli Fire reburned portions of the Cleveland burn. Managers attributed increased surface fuel continuity in the St. Pauli Fire to cheatgrass that established after the Cleveland Fire (Taylor 2003, personal communication cited in [319]).

Nonnative perennial or annual grasses are sometimes used to provide temporary ground cover to reduce erosion until native plants establish. However, postfire seeding of nonnative grasses may lower diversity of native species and is often ineffective at reducing erosion (review by [78]). On the Payette National Forest near Lowman, Idaho, a mix of nonnative intermediate wheatgrass, orchardgrass, smooth brome, and timothy was seeded-in after a wildfire that burned in low-elevation ponderosa pine, midelevation Douglas-fir, and high-elevation subalpine fir-Engelmann spruce habitat types. Cover of the nonnative grasses peaked in postfire year 4 and declined thereafter in all habitat types except ponderosa pine, where seeded grass cover remained stable and was dominated by orchardgrass. For all habitat types, seeded areas supported significantly less cover of native vegetation (shrubs, perennial herbs, and annuals) compared to adjacent unseeded areas ($P < 0.05$) [206]. Two years after postfire seeding of annual rye on the Lone Pine burn in south-central Oregon, species richness of native herbs was less on seeded than on unseeded plots, and seeding had not visibly reduced either rate of erosion or establishment of invasive nonnative herbs [492].

Surrogate Fire Studies

Fire surrogates are nonfire management tools, such as thinning and mastication, that are used to reduce fuel loads and mimic some features of wildland fire [324]. Fire managers may elect to use fire surrogates in areas where application of fire may not be feasible (e.g., wildland-urban interfaces) or to facilitate later reintroduction of fire. By reducing stand density and removing ladder fuels, thinning alone can reduce the possibility of crowning [38, 102, 265, 407]. However, thinning does not substantially reduce understory and litter layers [102].

Thinning from below may not be sufficient to restore historical stand structure to ponderosa pine stands. A study using FIA data for treated ponderosa pine stands across western Montana found that among three fire surrogate treatments, thinning from below to remove ladder fuels was least effective in reducing stand density and fire hazard. Treatments were:

A) thinning from below, removing trees ≤9 inches (23 cm) diameter; applied only in stands with density of >50 feet^2/acre (12 m^2/ha) of trees that were >9 inches in diameter;
B) 50% basal area removal, removing smaller half of basal area; or
C) thinning to basal density of 40-50 feet^2/acre (9-12 m^2/ha), mostly leaving large, fire-resistant tree species and removing late-successional species; leaving some trees in all diameter classes as advanced regeneration [172].

Because it comprehensively treated stand density, structure, and composition, the authors considered treatment C most effective. Projections over the next 30 years suggest that while the benefits of all treatments will diminish over time, fire hazard will be less under treatment C than under treatments A or B [172].

MANAGEMENT CONSIDERATIONS

FEDERAL LEGAL STATUS

None

OTHER STATUS

A preliminary report by the National Biological Service categorizes old-growth ponderosa pine ecosystems as endangered in the Northern Rocky Mountains, the Intermountain West, and the East Cascades due to fire exclusion and past selective logging [418].

IMPORTANCE TO WILDLIFE AND LIVESTOCK

Summary: Numerous wild animals use ponderosa pine stands for foraging, cover, and breeding habitat; and ponderosa pine communities are used as rangelands for livestock. Riparian ponderosa pine communities are extremely important habitat for many mammals and birds; they support some of the most diverse bird communities in North America [238].

Wildlife

Large and small mammals [218, 428], birds [238, 467], fish [453], and insects [334, 483] use ponderosa pine habitats and feed on ponderosa pine seeds and/or browse. For example, American black bears den in ponderosa pine logs and favor ponderosa pine catfaces for claw sharpening [29]. Elk ([361, 382], review by [285]), mule deer ([218], review by [286]), and white-tailed deer ([194], review by [287]) use ponderosa pine habitats for foraging and cover, especially in early postfire succession when shrub sprouts are abundant [361]. In the central and southern Sierra Nevada, fisher habitat is concentrated in and near large, old stands of ponderosa pine and mixed conifers, especially in areas supporting California black oaks ([516], review by [397]).

Some bat species favor early postfire habitats. A study comparing bat use of a first-year burn and an unburned mixed-conifer site on the Sequoia and Inyo national forests found that small bat species (e.g., fringed myotis) preferred hunting in areas that burned at high severity. Large bats (e.g., pallid bat) showed no habitat preferences (*P* = 0.05) [95].

See the Wildlife section of Fire Management and applicable FEIS wildlife Species Reviews for details on managing fire for wildlife.

Foraging

Many animals eat ponderosa pine seeds including American black (review by [549]) and grizzly bears; chipmunks, ground squirrels, and squirrels [218, 230, 474, 493]; and chickadees, crossbills, nuthatches, jays [154, 218, 230, 474, 493], and woodpeckers ([154, 218, 230, 474, 493], review by [531]). Over 8 months, Eastman [154] observed 18 bird species feeding on ponderosa pine seeds in eastern Oregon (*n* = 1,152 individuals).

Figure 16—A female red-breasted nuthatch holding a partially opened ponderosa pine seed. Creative Commons image by Blalonde.

Large mammals, lagomorphs, rodents, and birds browse ponderosa pine seedlings. Timing of dark-eyed junco migrations in Oregon [154] and western Montana [493] corresponds to emergence of ponderosa pine seedlings in spring, when they feed on emerging seedlings [493] and fall, when they feed on seeds [154].

Most mammals do not browse ponderosa pine needles and twigs unless other forage is scarce. Ungulates may browse ponderosa pine needles and twigs in winter [44]. North American porcupines eat the inner bark (cambium) [218].

In avian communities, feeding guilds change as postfire succession advances in ponderosa pine communities [376]. Bark probers, gleaners, flycatchers, and hoverers—such as nuthatches and woodpeckers; flycatchers; and bluebirds, respectively—prefer burns in early succession. Understory foragers such as quail and winter wrens prefer more closed canopies [48, 376]. On 50 sites in western

Montana, black-backed woodpeckers, three-toed woodpeckers, and mountain bluebirds were positively associated with 1- and 2-year-old burns ($P < 0.01$) [281].

Over 200 insect species feed on all aboveground parts of ponderosa pine, from the seedling to old growth stages of the tree's life [334, 483]. Ants nest in live and dead ponderosa pines, and beetle larvae live in and feed on live and dead ponderosa pines [9].

Ponderosa pine is a good host for pine beetles (*Dendroctonus* spp.) and other bark beetles. In a common garden study of mountain pine beetles in Oregon, larval development was faster and females larger in ponderosa pine hosts than in Rocky Mountain lodgepole, western white pine, or whitebark pine hosts. However, brood production rate was greatest in western white pine and whitebark pine hosts ($P = 0.05$ for all variables) [18].

Old Growth and Snags for Wildlife

Old-growth ponderosa pine and ponderosa pine snags are important sources of food and cover for wildlife ([49], review by [209]). Woodpeckers seek decayed, live ponderosa pines or snags to forage for insects [244]. Woodpeckers and other cavity nesters prefer ponderosa pines infected with heart-rot fungi; often, these are living trees with broken, dead tops [97].

Woodpeckers and most wood-feeding insects only forage in ponderosa pine snags early-on in a snag's residence. On the Starkey Experimental Forest in northeastern Oregon, woodpeckers fed on 82% of *Pinus ponderosa* var. *ponderosa* snags 1 year following a mountain pine beetle outbreak. They excavated nests 3 to 8 years after the outbreak, selecting trees >10 inches (26 cm) DBH and preferring trees >20 inches (52 cm) DBH with broken tops [96]. Woodpeckers observed using ponderosa pine snags included hairy woodpeckers, northern flickers, pileated woodpeckers, white-headed woodpeckers, and Williamson's sapsuckers [96, 244].

Livestock

Ponderosa pine communities are used for livestock grazing [257, 258, 332, 427]. Open structure provides more forage and access for cattle than late-successional or closed ponderosa pine stands [257]. Cattle preferentially select ponderosa pine riparian areas for foraging and loafing. On the Blodgett Forest Research Station in the Sierra Nevada, cattle on ponderosa pine rangeland preferred foraging first in riparian areas, then in clearcuts, second-growth forest, and burned areas, respectively [332].

Palatability and Nutritional Value

Ponderosa pine browse is generally unpalatable to ungulates [146]. Elk, deer, and bighorn sheep may browse the stems and bark when food and/or water are scarce [44, 199].

Ponderosa pine needles are bitter, and they are toxic to livestock. Cattle usually only browse the needles in winter, and only on rangelands where little other forage is available. Pregnant cows that eat ponderosa pine needles may abort their calves, and they may die because the placenta is often retained. These complications can arise after ingestion of only small amounts of ponderosa pine needles [290].

Sugar content of ponderosa pine cambium is high in the spring but becomes increasingly bitter as the growing season advances, likely because terpene levels increase [62].

Ponderosa pine browse is not very nutritious. Nutritional value of the browse and litter declines as plant parts age. A study in northern California found ponderosa pine litter in an old-growth forest was significantly lower in nitrogen than litter from young-growth plantation ($P = 0.001$) [251]. Stark [519] provides information on the nutritional value of ponderosa pine browse collected on Lubrecht Experimental Forest, including 1-year green needles, twigs, small branches, and large branches.

Cover Value

Summary: At every age class, ponderosa pine provides habitat for many mammals and birds. Seedlings provide low ground cover for small mammals and birds. Pole-size stands provide windbreaks and thickets important as hiding cover for large mammals. Mature trees and snags house arboreal species, including upper bole and branch cavity nesters. Fallen logs and stumps provide large cavity-using species such as bears with shelter.

Bears (review by [549]), ungulates (reviews by [285, 286, 287]), and small mammals use ponderosa pine habitats for cover. Elk and deer use ponderosa pine habitats for winter range, with ponderosa pine providing thermal and escape cover (reviews by [285, 286, 287]). On the Sierra National Forest, fishers denned and loafed in large ponderosa pines more often than expected based on their availability ($P = 0.002$). Selected trees were usually infected with western dwarf mistletoe [445]. Foxes den in downed trees or decaying live ponderosa pines [9]. Cottontails and ground-dwelling rodents use fallen logs and stumps for cover [266, 426]. However, fires were so frequent in most presettlement ponderosa pine forests that downed logs were probably historically fewer than in contemporary forests, because logs were consumed by successive fires.

Both large and small birds use ponderosa pine stands for cover. Eastern wild turkeys use ponderosa pine habitats year-round but especially in autumn, when they roost in branches by night and forage for ponderosa pine seeds by day [167]. Raptors build stick-pile nests in stout ponderosa pine branches or broken tops [49, 167]. Northern [200] and California [414, 569] spotted owls use ponderosa pine and Douglas-fir-ponderosa pine stands for hunting, roosting, and nesting [77, 200]. A review reports that 78% of all known northern goshawk nesting areas in the West are in ponderosa pine or Douglas-fir forests [86].

Birds that nest in ponderosa pine cavities include bluebirds, chickadees, nuthatches, [49, 415, 599], and woodpeckers [49, 96, 415, 467, 599]. Pygmy nuthatches, black-backed woodpeckers, and pileated woodpeckers select ponderosa pines preferentially for nesting [415]. On plots in mixed-conifer forests on the Sierra National Forest, for example, woodpeckers selected ponderosa pines for nesting more often than associated conifers and oaks (35% of total) [49].

Some cavity-nesting bird species prefer new burns as habitat [269, 283]. Following the 2003 Black Mountain Fire near Missoula, Montana, there was a significant difference among bird species in time-since-fire use of forage and nesting habitats. Black-backed and hairy woodpeckers, mountain bluebirds, and western wood pee-wees were detected most often in postfire years 1 and 2, while dusky grouse, Lewis' woodpeckers, and rock wrens were detected most often in postfire years 11 to 12. Birds also selected habitat based on fire severity. Dusky grouse, Lewis' woodpeckers, and rock wrens used high-severity burn patches more than expected based on availability, while dark-eyed juncos, Swainson's thrushes, and western tanagers used low-severity burn patches more often than expected ($P < 0.05$) [283].

Salvage logging may reduce habitat quality of cavity nesters [283]. On the Blackfoot-Clearwater Wildlife Management Area near Missoula, Montana, a mixed-conifer forest that burned in an October 1991 wildfire was salvage logged that winter (1991-1992). Diversity and density of cavity-nesting birds was higher in unlogged than salvage-logged plots. Some woodpeckers, including back-backed woodpeckers, three-toed woodpeckers, red-naped sapsuckers, and Williamson's sapsuckers, nested only in trees on unlogged plots. Other species, including house wrens, mountain bluebirds, and northern flickers, nested in trees on salvage-logged and unlogged plots but preferred trees on unlogged plots ($P < 0.05$) [269].

Salmonids and other fish depend on ponderosa pine communities for overhead shade and stream cover (large woody debris). Severe fire can remove this habitat in the short term. A study in Boise Basin conducted soon after wildfires in 1992 found that redband trout and bull trout were eliminated from stream reaches in *Pinus ponderosa* var. *ponderosa* habitats where fire was severe. By 1993, both fish species were repopulating burned stream reaches in the severely burned areas [453].

VALUE FOR RESTORATION OF DISTURBED SITES

Ponderosa pine is widely used for soil stabilization and watershed protection [557]. Because it is deep-rooted, it provides superior watershed protection [209].

OTHER USES

Ponderosa pine is a valuable timber tree [34]. Old trees produce smooth, fine-grained wood, although the wood of young trees is coarse and warps when dried [29, 167].

Ponderosa pine has high aesthetic value. It is the iconic tree of the West; large trees impart a spiritual feeling in most who visit ponderosa pine forests [209]. Ponderosa pine stands offer year-round aesthetic scenery and recreation [422].

Ponderosa pine forests are desirable places to live. Historically, many American Indian villages were located ponderosa pine forests; today, many people live in ponderosa pine wildland-urban interfaces [168].

American Indians traditionally and still utilize many pine materials. For example, they collected and ate ponderosa pine seeds [405, 601]; the inner bark was stripped and also used as food [62, 405]. Some old ponderosa pines with such stripped bark are still standing in forests of the West; these trees are considered living archeological treasures [62] (see figure 1). Ponderosa pine needles were used in basketry, and the pitch as glue. The bark was used a roofing material, and the poles in lodge construction [70, 405].

American Indians utilized many understory species that grow in ponderosa pine stands for food and for making tools and utensils (e.g., thimbleberry and red-osier dogwood). They burned some ponderosa pine stands frequently in order to maintain ponderosa pine and favored understory species. Lake [351] stated that tribal peoples managed for large ponderosa pines, sugar pines, and California black oaks preferentially over Douglas-firs and other shade-tolerant conifers.

OTHER MANAGEMENT CONSIDERATIONS

Old-growth ponderosa pine ecosystems are in decline throughout the West. This is attributed to fire exclusion; succession to late-seral, shade-tolerant conifer species; overharvesting; and on some sites, overgrazing [296, 418, 447]. As a result, many contemporary ponderosa pine forests exhibit slow growth and production, decreased nutrient cycling and biodiversity, increased soil erosion, and increased rates of disease compared to presettlement ponderosa pine forests [447].

For example, Lutz et al. [370] found that large ponderosa pines were declining disproportionately at the lowest elevations of their range in Yosemite National Park. Density of large-diameter ponderosa pines (>36 inches (91 cm) DBH) was compared from 1932-1936 surveys and 1998-1999 surveys. Across the park, density of large ponderosa pines averaged 6.2 trees/acre (15.4/ha) in the early surveys compared to 2.8 trees/acre (6.9/ha) in the later surveys. This was a 55% reduction in density of large ponderosa pines ($P = 0.017$). In the later surveys, density of large-diameter conifers was similar in plots that had burned since the 1932 and plots that had not. However, large-diameter ponderosa pines dominated burned plots, while large-diameter incense-cedar and white fir dominated plots that had not burned since 1932 [370].

Ponderosa pine is subject to attack by bark beetles, pine white butterflies, and a host of other insect pests. These linked references provide reviews of insects [176, 261, 483] and major pathogens [97, 256] affecting ponderosa pine health.

APPENDICES

Table A1: Common and scientific names of plant species. Links go to FEIS Species Reviews.

- Trees
- Shrubs
- Graminoids
- Forbs

Common name	Scientific name
Trees	
Arizona pine	*Pinus arizonica*
bigcone Douglas-fir	*Pseudotsuga macrocarpa*
bigleaf maple	*Acer macrophyllum*
California black oak	*Quercus kelloggii*
canyon live oak	*Quercus chrysolepis*
cottonwoods	*Populus* spp.
Coulter pine	*Pinus coulteri*
Douglas-fir	*Pseudotsuga menziesii*
Rocky Mountain Douglas-fir	*P. menziesii* var. *glauca*
coast Douglas-fir	*P. menziesii* var. *menziesii*
Engelmann spruce	*Picea engelmannii*
firs	*Abies* spp.
grand fir	*Abies grandis*
gray pine	*Pinus sabiniana*
incense-cedar	*Calocedrus decurrens*
interior live oak	*Quercus wislizeni*
Jeffrey pine	*Pinus jeffreyi*
lodgepole pine	*Pinus contorta*
Rocky Mountain lodgepole pine	*P. contorta* var. *latifolia*
Sierra lodgepole pine	*P. contorta* var. *murrayana*
oaks	*Quercus* spp.
Oregon white oak	*Quercus garryana*
Pacific madrone	*Arbutus menziesii*
pines	*Pinus* spp.
ponderosa pine	*Pinus ponderosa*
Pacific ponderosa pine	*P. ponderosa var. benthamiana* (this review)
southwestern ponderosa pine	*P. ponderosa var. brachyptera*
Columbia ponderosa pine	*P. ponderosa var. ponderosa* (this review)
Rocky Mountain ponderosa pine	*P. ponderosa var. scopulorum*
Washoe pine	*P. ponderosa var. washoensis*
red fir	*Abies magnifica*
Rocky Mountain juniper	*Juniperus scopulorum*
Sierra juniper	*Juniperus grandis*
subalpine fir	*Abies lasiocarpa*
sugar pine	*Pinus lambertiana*
tanoak	*Notholithocarpus densiflorus*
western juniper	*Juniperus occidentalis*

western larch	*Larix occidentalis*
western white pine	*Pinus monticola*
white fir	*Abies concolor*
whitebark pine	*Pinus albicaulis*
willows	*Salix* spp.
Shrubs	
antelope bitterbrush	*Purshia tridentata*
big sagebrush mountain big sagebrush	*Artemisia tridentata* *A. tridentata* subsp. *vaseyana*
Bloomer goldenbush	*Ericameria bloomeri*
buckbrush	*Ceanothus cuneatus*
common snowberry	*Symphoricarpos albus*
creeping snowberry	*Symphoricarpos mollis*
curlleaf mountain-mahogany	*Cercocarpus ledifolius*
deer brush	*Ceanothus integerrimus*
Douglas hawthorn	*Crataegus douglasii*
dwarf rose	*Rosa gymnocarpa*
Greene's mountain-ash	*Sorbus scopulina*
greenleaf manzanita	*Arctostaphylos patula*
Lewis' mock orange	*Philadelphus lewisii*
mallow ninebark	*Physocarpus malvaceus*
manzanita	*Arctostaphylos* spp.
mountain misery	*Chamaebatia foliolosa*
Pacific poison-oak	*Toxicodendron diversilobum*
pipsissewa	*Chimaphila umbellata*
prostrate ceanothus	*Ceanothus prostratus*
red-osier dogwood	*Cornus sericea*
Rocky Mountain maple	*Acer glabrum*
sagebrush	*Artemisia* spp.
Saskatoon serviceberry	*Amelanchier alnifolia*
snowbrush ceanothus	*Ceanothus velutinus*
sticky whiteleaf manzanita	*Arctostaphylos viscida*
western dwarf mistletoe	*Arceuthobium campylopodum*
white spirea	*Spiraea betulifolia*
Graminoids	
alpine rough fescue	*Festuca campestris*
annual rye	*Secale cereale*
blue wildrye	*Elymus glaucus*
bluebunch wheatgrass	*Pseudoroegneria spicata*
California needlegrass	*Achnatherum occidentale* subsp. *californicum*
cheatgrass	*Bromus tectorum*
Chewing's fescue	*Festuca rubra* subsp. *fallax*
Idaho fescue	*Festuca idahoensis*
intermediate wheatgrass	*Thinopyrum intermedium*
Lemmon's needlegrass	*Achnatherum lemmonii*

needle-and-thread grass	*Hesperostipa comata*
orchardgrass	*Dactylis glomerata*
pinegrass	*Calamagrostis rubescens*
Ross' sedge	*Carex rossii*
sedges	*Carex* spp.
sixweeks grasses small sixweeks grass rattail sixweeks grass sixweeks grass	*Vulpia* spp. *V. microstachys* *V. myuros* *V. octoflora*
smooth brome	*Bromus inermis*
timothy	*Phleum pratense*
ventenata	*Ventenata dubia*
western needlegrass	*Achnatherum occidentale*
Forbs	
bull thistle	*Cirsium vulgare*
Canada thistle	*Cirsium arvense*
common mullein	*Verbascum thapsus*
houndstongue	*Cynoglossum officinale*
miner's-lettuce	*Claytonia perfoliata*
musk thistle	*Carduus nutans*
sidebells wintergreen	*Orthilia secunda*

Table A2—Stand structure of ponderosa pine stands in Oregon and California. Cells are blank where information was not available.

Area	Metolius Research Natural Area, OR [596]	Ishi Wilderness, Lassen NF, CA [456]	Blacks Mountain Experimental Forest, Lassen NF, CA [456]	Tahoe and Stanislaus national preserves[a], CA [532]
Period	1995-1997	1750-1904	1933-1934	1900
Stand age (years)	37-618			250-350
Stand density: stems/acre (stems/ha)	Canopy: 14-38/acre (34-94/ha)			
	Subcanopy: 179-1,341/acre (443-3,313/ha)			
DBH	25.2 inches (63.9 cm)		Large ponderosa: >22.8 inches (58 cm)	3 to 4 feet (0.9-1.2 m)
			Midsize ponderosa: 11-22.8 inches (28-58 cm)	
			Sapling ponderosa: 3.5-11 inches (9-28 cm)	
Canopy height				150- 180 feet (46-55 m)
Patch size	72 feet (22.5 m) diameter	301 feet^2-0.25 acre (28 m^2-0.1 ha)		
Age structure	uneven-aged	uneven-aged	uneven-aged	mostly even-aged

[a] Now the Tahoe and Stanislaus national forests.

Table A3—Historical and contemporary stand structure of unlogged conifer communities on the Klamath Indian Reservation, Oregon, in which ponderosa pine was historically dominant or codominant. White fir historically dominated mixed-conifer communities, and continues to do so. Snowbush ceanothus dominates the understories of dry mixed-conifer communities; Saskatoon serviceberry, snowbush ceanothus, or sedges dominate those of moist mixed-conifer communities. Continuous Vegetation Survey (CVS) data are restricted to conifers ≥6 inches (15 cm) DBH. Numbers in parentheses are standard deviation and range (SD, range) [223].

Variable	Timber Inventories 1919-1922				Contemporary Vegetation Surveys (CVS) 1997-2006			
	Ponderosa pine	Mixed- dry	Mixed- moist	All	Ponderosa pine	Mixed- dry	Mixed- moist	All
Number of plots	1,539	562	966	3,068	55	24	12	95
Plot area (ha)	3,276	1,186	2,182	6,646	55	24	12	95
Basal area								
All species (m^2/ha)	13 (5, 0-28)	17 (8, 2-55)	19 (8, 0-83)	16 (7, 0-83)	17 (8, 0-34)	24 (7, 8-37)	24 (12, 11-55)	19 (9, 0-55)
% ponderosa pine	96 (19, 0-100)	87 (16, 36-100)	19 (8, 0-100)	78 (21, 0-100)	85 (18, 21-100)	39 (24, 4-82)	20 (19, 0-65)	63 (33, 0-100)
Basal area of large conifers (≥21 inches (53 cm DBH))								
All species (m^2/ha)	10 (5, 0-28)	15 (8, 1-54)	16 (8, 0-78)	13 (7, 0-78)	5 (4, 0-16)	8 (5, 0-21)	10 (11, 2-41)	6 (6, 0-41)
% of total BA	80 (18, 0-100)	88 (11, 36-100)	83 (16, 0-98)	83 (16, 0-100)	27 (19, 0-80)	33 (19, 0-83)	39 (19, 7-74)	30 (19, 0-83)
% ponderosa pine	99 (15, 0-100)	87 (17, 31-100)	65 (26, 0-100)	81 (20, 0-100)	91 (20, 0-100)	41 (35, 0-100)	36 (27, 0-76)	67 (37, 0-100)
% white fir	0 (1, 0-35)	4 (6, 0-31)	27 (26, 0-100)	13 (16, 0-100)	2 (9, 0-55)	24 (25, 0-100)	54 (33, 0-100)	15 (26, 0-100)
Conifer density by species								
All species (stems/ha)	63 (24, 1-225)	64 (22, 14-156)	78 (37, 0-296)	68 (29, 0-296)	217 (121, 0-543)	286 (130, 109-572)	233 (90, 104-378)	234 (122, (0-572)
% ponderosa pine	81 (26, 0-100)	85 (18, 14-100)	45 (29, 0-100)	67 (26, 0-100)	81 (24, 5-100)	34 (25, 4-83)	15 (23, 0-85)	59 (36, 0-100)
% white fir	0 (0, 0-22)	4 (7, 0-35)	45 (7, 0-35)	19 (0, 0-100)	1 (3, 0-10)	40 (26, 2-81)	80 (24, 13-100)	21 (32, 0-100)
% lodgepole pine	19 (27, 0-100)	8 (16, 0-86)	6 (14, 0-100)	13 (22, 0-100)	14 (24, 0-95)	1 (3, 0-14)	1 (3, 0-9)	9 (20, 0-95)
Overall conifer density								
trees <53 cm DBH (trees/ha)	38 (26, 0-211)	29 (20, 0-117)	43 (30, 0-117)	38 (27, 0-227)	205 (119, 0-531)	265 (131, 96-560)	207 (94, 92-357)	217 (121, 0-560)
trees ≥53 cm DBH (trees/ha)	12 (9, 0-42)	21 (12, 0-45)	26 (30, 4-114)	16 (15, 0-114)	24 (11, 0-56)	35 (16, 3-105)	35 (17, 0-147)	30 (14, 0-147)
% trees ≥53 cm DBH	7 (6, 0-28)	9 (7, 0-32)	12 (14, 1-52)	8 (8, 0-52)	39 (2, 0-100)	55 (2, 0-100)	45 (4, 0-96(	44 (10, 0-100)
% of area with ≥25 trees/ha that are ≥53 cm	5	38	25	17	42	76	71	58

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