



Fire Resistance and Regeneration Characteristics of Northern Rockies Tree Species

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Hood, Sharon; Abrahamson, Ilana; and Cansler, C. Alina. 2018. Fire resistance and regeneration characteristics of Northern Rockies tree species. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). Available: <https://research.fs.usda.gov/sites/default/files/2025-05/feis-FireResistRegen.pdf>

Wildfire is a common occurrence in the Northern Rockies and many tree species have adaptations to survive and regenerate after fire. The following information provides a general understanding of fire resistance and regeneration traits and strategies. This information is important for predicting how fire will impact trees in an area and how forest succession and future disturbance processes will influence the development of stands with and without management actions. This information, in combination with the Post-fire Assessment of Tree Status Report 17-17 v2.0, can be used to evaluate the relative likelihood that a tree species will survive or die within 3 years from fire-related injuries and expected post-fire regeneration response. Tables 1 and 2 provide summary information of 11 conifer species characteristics that influence their degree of resistance to fire and regeneration traits. Figure 1 estimates the probability of seedling establishment based on distance to seed source for four conifers in the Northern Rockies. More detailed information is listed by species below.

Table 1. Relative fire resistance of tree species ranked from high to low resistance based on Smith and Fischer (1997), Peterson and Ryan (1986), Minore (1979), and Flint (1925). Notes in parentheses indicate where rankings differed between Minore (1979) and Flint (1925).

Species	Bark thickness of large trees	Bark thickness on small trees	Root habit	Branch habit	Stand habitat	Relative flammability of foliage	Lichen growth	Degree of fire resistance
Western larch	Very thick	Thick	Deep	High & very open	Open	Low	Medium to heavy	Most resistant
Ponderosa pine	Very thick	Thick	Deep	Moderately high & open	Open	Medium (low)	Medium to light	Very high
Douglas-fir	Very thick	Thick	Varies, usually deep	Moderately low & dense	Moderate to dense	High	Heavy to medium	High when mature
Grand fir	Medium	Thin	Varies	Low & dense	Dense	High (medium)	Heavy (medium)	Medium
Western white pine	Thin	Very thin	Medium	High & dense	Dense	Medium	Heavy (Medium)	Medium
Western redcedar	Thin	Very thin	Shallow	Moderately low & dense	Dense	High	Heavy (medium)	Medium
Whitebark pine	Thin	Very thin	Deep	High and open	Open	Medium	Moderate	Low
Lodgepole pine	Very thin	Very thin	Deep	Moderately high & open	Open	Medium	Light	Low
Western hemlock	Medium	Thin	Shallow	Low & dense	Dense	High	Heavy	Low
Engelmann Spruce	Thin	Very thin	Shallow	Low & dense	Dense	Medium (high)	Heavy	Very low
Subalpine fir	Very thin	Very thin	Shallow	Very low & dense	Moderate to dense	High	Medium to heavy	Very low

Table 2. Regeneration characteristics of tree species ranked from high to low fire resistance (Table 1). Adapted from Kemp et al. (2016), Minore (1979), McCaughey et al. (1986), and Fire Effects Information System Species Reviews.

Species	Age to maturity (years)	Seed production	Seed dispersal distances	Germination requirements	Seedling survival
Western larch	25, heavier crops after 40-50	Seed produced annually, and large crops every 5 years	50% of seeds dispersing >150 ft, 20% of seeds dispersing >360 ft	Greatest on mineral soils with high light	Best in high light
Ponderosa pine	4-8	Large seed crops produced every 2-8 years	50% of seeds dispersing >80 ft, 20% of seeds dispersing >200 ft	Highest germination on mineral soil or ash	Best in high light and mineral soil
Douglas-fir	12-15	Seed produced annually; large crops every 2-11 years	3 percent of seeds dispersing >260 ft	Establishes in mineral soil and organic seedbeds with high light	Best in partial shade in dry habitats
Grand fir	20-50	Heavy cone production is followed by several years of light production	The winged seeds are of medium weight compared to other conifers and are wind-dispersed a few hundred feet from the parent	Greatest on ash or mineral soils. Established in light to moderate understory shade	Drought is a major cause of seedling mortality
Western white pine	7-20	Large seed crop every 3-4 years	Most seeds fall within 390 ft of the parent tree, but have been recorded at over 2,620 ft	Greatest on mineral soils, but will also germinate in the duff	On dry sites seedling establishment is favored by partial shade, while on moist sites full sunlight favors establishment
Western redcedar	20-30	Large seed crops every 3-4 years	<400 ft from parent tree	Highest on mineral soil	Best in partial shade
Whitebark pine	20-30	Large seed crops every 3-4 years	All seeds are disperse by wildlife (Clark's nutcracker). Seed dispersals up to 20 miles have been recorded	Best in severe burns and on mineral soil. Seed germination can be delayed for multiple years; best germination may occur 2 years after good cone crop	Best on moderately to severely burned moist sites. Gophers and other wildlife can cause mortality.
Lodgepole pine	5-15	Large seed crops every 1-3 years. Seed persists in the canopy	50% of seeds dispersing >60 ft, 20% of seeds dispersing >140 ft	Highest on mineral soil and in full sunlight	High temperatures and drought may kill seedlings
Western hemlock	25-30	Seed produced annually, and large crops every 3-4 years	50% of seeds dispersing >295 ft, 20% of seeds dispersing >395 ft	Germinates well on most natural seedbeds	Very shade tolerant but sensitive to heat, cold, drought and wind
Engelmann Spruce	15-40	Large seed crops produced every 2-5 years	50% of seeds dispersing >90 ft, 20% of seeds dispersing >200 ft	High germination rates (69%), occasional germination delayed until after summer rain or second year. Germinates best on moist mineral soil with partial shade	Seedlings survive best under conditions of shade, cool temperatures, and adequate soil moisture
Subalpine fir	Appx. 20; later under closed forest conditions	Large seed crops every 3-5 years; light seed crops of no seed crops in between	50% of seeds dispersing >100 ft, almost all seeds within 260 ft	Establish best on mineral soil seedbeds but will also establish on other surfaces including litter, duff, and decaying wood	At higher elevations, seedling survival greater on duff seedbeds. At lower elevations, seedling densities greater on mineral soils

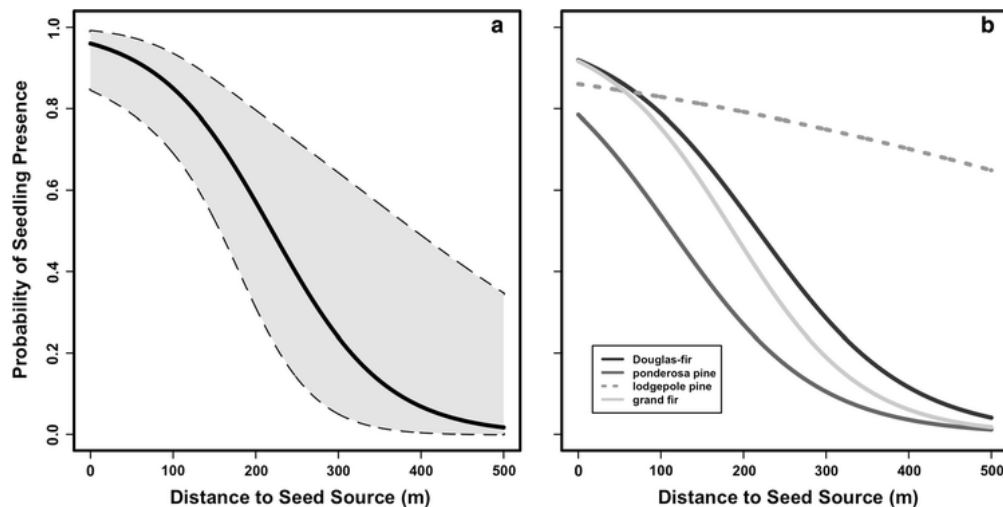


Figure 1. Relationship between the probability of seedling presence and distance to a live seed source for (a) all species and (b) the four most abundant species from a study on conifer regeneration in the Northern Rockies, when all other variables in the model are held at their median values. The shaded region between the *dotted lines* represents the 95 % confidence intervals on the predicted values for the all species model. In panel (b), the *dashed line* indicates that the relationship between distance and seedling presence was not significant for that species ($p > 0.05$). Confidence intervals are not shown in panel (b) because they overlap for all species. From Kemp et. al. 2016.

The information presented in the following species summaries comes from Fire Effects Information System (FEIS) reviews unless otherwise referenced. Primary citations used in FEIS reviews have been removed from this report. See full FEIS reviews for more detailed information.

Western Larch

Western larch is the most fire-resistant species in the Northern Rockies. While seedlings, saplings, and poles are somewhat susceptible to fire, trees >150 old are able to survive all but the most severe fires, such as when smoldering ground fires cause basal stem and root death or when buds are killed by crown fire (Smith and Fischer 1997). It is common for a handful of mature western larch trees to be the sole survivors after fire. Western larch's characteristic high, open crown; open stand habit; and self-pruning lower branches reduces ladder fuels and risk of crown fire. Bark in mature trees is thick and furrowed into large, flaky plates. At age 50, basal bark thickness ranges from 5" to 10", increasing to 10" to 18" by age 100. Bark char is not a reliable indicator of underlying stem death due to thick bark (Hood et al. 2008). Its deep roots are protected from surface fires. Needles of western larch are less flammable than other species' due to their small size. Because they are never more than 5 months old, larch needles maintain a higher water content than other conifers' needles, which are replaced every 2+ years. Heat-resistant woody bud scales allow higher bud survival compared to other species even when needles are killed (also called crown scorch) from convective heating during fire. Because western larch is deciduous and, therefore, annually replaces its needles, it is better able to survive nearly complete defoliation from crown scorch if buds are not killed compared to other conifers.

Fire is an important part of western larch's ecology; without fire or other stand replacing disturbance, western larch will not regenerate successfully and will eventually be replaced by more shade-tolerant species. Western larch is the least shade-tolerant conifer in its range. Western larch cone production may begin as early as age 8, though it is unusual on trees less than 25 years old. Heavier crops usually begin at approximately 40 to 50 years of age and continue for 300 to 500 years. Trees usually produce cones annually, but crop size varies with year and location; heavy cone crops occur every 5 years on average. Western larch seeds are viable one year following fertilization. Seeds are very light and long-winged, allowing trees in nearby stands to reseed even if no onsite seed source is present. Most seeds fall within 328 feet of the parent. Depending on wind conditions, dispersal may be even longer, up to 820 feet or more. Cone-producing western larch survivors quickly reseed burned-over areas; on mineral soil seedlings develop rapidly and outgrow competitors. Fire-killed trees may contribute to seeding if fresh cones in the burned crown mature and disperse seed. However, dispersed seed can be destroyed by fires that occur in early fall. Since western larch is a long-lived and fire-resistant species, surviving trees serve as a potential seed source for centuries once they are established.

Ponderosa Pine

Ponderosa pine of all age classes are resistant to low- and moderate-severity surface fires. Even in the seedling stage, ponderosa pines are more fire-resistant than seedlings of associated conifer species. Unless growing in clumps, saplings and pole-sized ponderosa pines generally survive surface fires. Branches are pruned by surface fires, reducing probability of future crown fire. Specific adaptations to fire include thick bark, a high, open crown, self- and fire-pruned branches, large, protected buds, high foliar moisture content, deep roots, and rapid root growth of seedlings. Ponderosa pines begin to develop insulating bark when they reach about 2" in diameter; this provides enough protection to survive most surface fires. Thick, platy, and fissured bark ≥ 3 " of mature ponderosa pines provides even further protection from fire. Light and moderate bark char ratings are indicative of living cambium due to thick bark (Hood et al. 2008). The taproot and large roots of ponderosa pine are deep on favorable sites. In sand or other porous soils, large roots may extend 6 feet deep or more, but are rarely more than 3 feet deep in heavy clay soil. Fine roots are typically shallow and short-lived. Large buds are shielded by thick, long needles, which increases resistance to convective heating and can allow bud survival even when needles are scorched and killed. In many fire-excluded areas, ponderosa pine and other early-seral, shade-intolerant tree species have been successional replaced by late-seral, shade-tolerant species. Stand structure has changed from a mostly single canopy layer to multiple canopy layers. In these long-unburned stands, altered stand composition and structure can increase fire intensity and kill mature ponderosa pine by causing high levels of crown scorch. Additionally, high fire severity can occur from smoldering ground fires in deep duff that can accumulate at the base of ponderosa pine. Under this situations, mature ponderosa pine can be damaged or killed even when fire intensity and crown damage is low due to damage to cambium at groundline and shallow roots (Hood 2010). Western pine beetle and mountain pine beetle can cause additional mortality in fire-injured trees, but little evidence exists that fire stimulate outbreaks in adjacent unburned areas (Davis et al. 2012). In fact, low-severity fire can stimulate ponderosa pine resin duct defenses and make it more difficult for attacking bark beetles to kill the tree (Hood et al. 2015).

Ponderosa pine regenerates mostly successfully after disturbances that open the canopy and

expose bare mineral soil. Fire is the primary agent creating these conditions. Ponderosa pine is shade intolerant and does not regenerate well in shade. Trees bear cones as early as 7 years, up to at least 350 years. Seeds from trees aged 60 to 160 are the most viable. Ponderosa pine is a mast seeding species; observations over 23 years in Montana show it is a poor seeder west, and a fair seeder east, of the Continental Divide. The average interval between heavy cone crops is 8 years. When cone crops do occur, squirrels along with cone and seed insects often destroy the crop prior to dissemination or unfavorable seedbeds reduce seedling survival. Ponderosa pine seed remains viable for about 6 months. Ponderosa pine seed is primarily dispersed by wind, but also from birds and mammals. The winged seeds are buoyant and carry for short distances, usually no more than 150 feet from the parent tree. Wind-dispersed seed overwinters in or on top of litter. Animal-cached seed may be stored in shallow soil seed banks. Highest germination rates occur on bare mineral soil or an ash seedbed.

Rocky Mountain Douglas-fir

Mature Douglas-fir is very fire resistant. However, Douglas-fir is slower growing and much less fire resistant than ponderosa pine or western larch in sapling and pole stages. High fire frequency reduces the dominance of Rocky Mountain Douglas-fir relative to western larch and ponderosa pine because of the species' differential rates of growth and susceptibility to fire. Seedlings, saplings, and pole-sized Douglas-fir trees are easily killed by surface fires because of thin bark, low branches, flammable needles and small buds (Smith and Fischer 1997). Trees develop fire-resistant bark in about 40 years that is about 12% of bole diameter on moist sites in the northern Rockies. This thicker, corky bark insulates cambium tissue from heat. Cambium is typically alive under bark with moderate bark char rating due to thick bark (Hood et al. 2008). Fire resistance offered by thick bark can be often offset by shallow roots and low-growing branches. Root morphology is variable, but when unimpeded, a taproot forms within several years. Frequently, Douglas-fir has major lateral roots at or near the interface between the organic and mineral soil and those roots can be killed if the organic layer is consumed (Ryan et al. 1988). Trees infected with Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) often accumulate dense brooms that increase likelihood of torching. Fine branch structure and small buds are susceptible to crown scorch.

Douglas-fire beetle and root disease are additional factors to consider when estimating post-fire effects. Douglas-fire beetle is an aggressive bark beetle species that can erupt to cause severe tree mortality when a catalyst (typically blowdown or a wildfire event) occurs in conjunction with ambient conditions favorable to Douglas-fire beetle population releases near suitable host trees. Suitable Douglas-fire stands contain older trees (>120 years in age) that are large-diameter (>14" DBH) and located in dense stands (especially those >250 feet² per acre of basal area) composed primarily of Douglas-fir (Egan et al. 2018). Bentz and Hood (2007) estimated Douglas-fire beetle caused an additional 25% mortality to fire-injured Douglas-fir trees $\geq 9"$ DBH that otherwise would have survived. Because Douglas-fire stands infected with root rot are predisposed to attack by Douglas-fire beetle, mortality after fire may be higher in areas with root disease and near existing Douglas-fire beetle populations.

Age at first reproduction is 12 to 15 years. Seed is usually produced annually, with abundant crops approximately every 2 to 11 years. Douglas-fir has winged seeds that are dispersed primarily by wind and gravity. Most seeds fall within 330 feet of their source, although seedfall

is possible from sources 0.6 to 1.2 miles away. Rocky Mountain Douglas-fir establishes in mineral soil and organic seedbeds less than 2" thick. Mineral soil exposed by burning provides a good seedbed. Most germination occurs within 150 days of seedfall, but seeds remain viable for 1 or occasionally 2 years. On xeric sites, establishment is more successful in shade.

Grand Fir

Grand fir has a medium level of fire resistance, primarily because large, old trees can have relatively thick bark. Young grand fir have thin bark and are easily killed by fire. Trees under 4" diameter at ground level are most susceptible to fire. Bark is thin on young trees (0.35" for a 7.9" DBH tree) and moderately thick at maturity (0.67" for a 15.7" DBH tree). Bark thickness is approximately 4.3% of the tree's DBH. The bark thickens as trees age, becoming up to 2" thick at maturity and providing moderate resistance to surface fires. Ground fires burning duff kill shallow roots, leading to death of even mature trees. Rooting characteristics vary by site conditions. On dry sites a well-developed taproot grows to moderate depths, while on moist sites shallow lateral roots prevail and the taproot may be absent. Depth of horizontal roots is moderate compared to associated conifers. Several morphological characteristics of grand fir lend to its relative flammability and increased susceptibility to fire. Its low, dense branching habit, flammable foliage, and tendency to develop dense stands with heavy lichen growth increase the likelihood of torching and mortality from crown fire. The foliage has a higher surface-to-volume ratio than that of associated conifers, and the needles are retained longer on the tree (average of 7 years). Fire-scarred grand fir are susceptible to heart rot, a problem that is more serious east of the Cascade Range crest because of the ubiquitousness of Indian paint fungus in the eastern portion of grand fir's range. Grand fir is also susceptible to fir engraver beetles and drought.

Grand fir is not as shade-tolerant as western red cedar, hemlocks, or other firs and does not establish beneath a closed canopy. Cone production begins at 20 to 50 years of age and increases with age. A year of heavy cone production is typically followed by several years of light production. The winged seeds are of medium weight compared to other conifers and are wind-dispersed within a few hundred feet of the parent. Grand fir regeneration is common after fire, showing good establishment on recently disturbed sites. Mineral soil or ash are the most favorable seedbeds. However, seedling mortality may be higher on burned soils due to higher surface temperatures on blackened compared to unburned soils. Grand fir also establishes in light to moderate understory shade and in small openings in mature forests. Mature grand fir that survive fire provide an on-site seed source. Seedlings often establish in the first few post-fire years. Because grand fir seedlings are not as drought tolerant as many conifer associates, grand fir establishment is sometimes slow or delayed by drought, but grand fir is usually established as a component of seral vegetation by 20 to 30 years after fire. Grand fir regeneration is also common after moderate-severity fire thins a dense overstory.

Western White Pine

Western white pine is not very fire resistant, and trees are often killed by cambium and crown damage. Young white pine trees are even more susceptible to being killed because of thin bark, retention of lower limbs, and dense stand structures (Smith and Fischer 1997). Mature trees do have some characteristics to resist fire such as medium-thick bark, moderately flammable foliage and the self-pruning of lower limbs. The bark on young trees is smooth and thin and becomes

slightly thicker on mature trees. Any bark charring is indicative of underlying dead cambium (Hood et al. 2008). Heat-killed cambium provides a vector for butt rots to enter the tree. The root system consists of a taproot and lateral roots which can spread up to 26 feet. Most (75 percent) of the lateral roots are in the upper 24" of soil. The large amount of humus in western white pine forests renders the trees susceptible to death from lethal heating to roots. In contrast, dense stands western white pine self-prunes, leaving a long, clean bole that can protect needles from crown scorch from surface fires. Western white pine is host to mountain pine beetle and additional mortality should be expected if beetle populations are nearby.

Western white pine is classified as shade intolerant to very intolerant. It can produce cones at a young age, with good seed crops occurring every 3 to 4 years. The seed is dispersed by wind up to 2,620 feet from the parent tree. Seeds remain viable in the duff for up to 4 years, but germination rate sharply decreases over time. Germination is best on mineral soil, but seeds will germinate in duff. After a stand-replacing fire, western white pine will seed in from adjacent areas. Cool to moderate fire that leaves a mosaic of mineral soil and duff, allows western white pine to reoccupy the site from seed stored in the seed bank. However, progeny originating from surviving mature white pine will likely have very low survival due to limited resistance to blister rust disease. Planting blister rust-resistant seedlings will increase the likelihood of western white pine recruitment.

Western Redcedar

Western redcedar fire resistance is low to moderate. Its thin bark, shallow root system, low dense branching habit, and highly flammable foliage make it susceptible to fire damage. Large western redcedar trees can survive if they are not completely girdled by fire, but younger trees rarely survive. Fire-scarred western redcedar can survive for a long time due to its ability to compartmentalize wounds and decay resistance. The bark is thin, fibrous and stringy or shreddy. Thickness varies from 0.5" to 1". Any bark charring is indicative of underlying dead cambium (Hood et al. 2008). Western redcedar roots are extensive. Tap roots are poorly defined or nonexistent, but fine roots develop a profuse, dense network. Root systems tend to be shallower and less extensive on wet soils than on deep, moderately dry soils. When a thick duff layer is present, many western redcedar roots grow in the duff rather than in the underlying soil, making them highly susceptible to surface fires. Fire injury to roots can lead to fungal infection, chronic stress, and growth losses. Western redcedar retains its lower limbs except when in densely crowded stands. The most common causes of fire mortality are root death and crown scorching.

Seed production normally begins when trees are 20 to 30 years old. However, open-grown trees may produce seed by age 10. Cones are often numerous and heavy seed crops occur every 3 to 4 years. The seeds are dispersed primarily by wind. Seeds have small wings and are not carried more than 400 feet from the parent tree. After fire, western redcedar will readily establish on bare mineral soil seedbeds via off-site wind-dispersed seeds and surviving trees. Mineral soil is a better seedbed in many environments than moss or duff, which may dry out rapidly. Regeneration grows best in partial shade, although may fail on heavily shaded sites due to poor root penetration.

Whitebark Pine

Whitebark pine has low resistance to fire. While individual are easily killed by fire, two strategies allow whitebark pine to survive in fire-prone ecosystems: survival of large and refugia trees, and post-fire seedling establishment facilitated by Clark's nutcrackers. Pole- and smaller-sized whitebark pine usually do not survive surface fires, but patchy fires resulting from fuel-limited whitebark pine habitats reduces mature whitebark pine mortality. In western Montana, whitebark pine with multiple fires scars dating from 1600 to 1900 are common, demonstrating ability to survive if fire does not completely encircle the tree. Bark thickness is thin, seldom reaching over 0.4". Bark charring is a reliable indicator that the underlying cambium is dead (Hood et al. 2008). Whitebark pine and mixed-conifer communities with a whitebark component experience fire frequently without suppression. Fire spread is inhibited due to discontinuous canopies and sparse understory fuels. Fire severity is low where surface fuels are sparse, and the resulting underburn kills mostly small trees and fire-susceptible overstory species. This type of patchy, discontinuous fire can allow mature whitebark pine to survive fire.

Cones are first produced at 20 to 30 years of age on good sites, but on most sites trees do not reach full cone production until 60 to 100 years of age. Peak cone production extends for another 250 years, then gradually declines. Some 1,000-year-old trees still reproduce. Cone production is characterized by frequent years of small cone crops and less frequent years of moderate to heavy crops. Whitebark pine is the only North American pine with a seed bank. Clark's nutcrackers prefer open sites with mineral soil for caching, and readily cache seed on large openings created by stand-replacement fire and in smaller openings created by mixed-severity fire. Due to seed caching by Clark's nutcrackers and delayed seed germination, whitebark pine may show good seedling establishment even if the previous year's cone crop was poor. Clark's nutcrackers have been observed caching seed as far as 20 miles from parent trees (Lorenz et al 2001). Seedling density on the Sleeping Child fire in western Montana decreased sharply as distance from seed source increased. Whitebark pine seedlings establish on open sites created by mixed-severity and stand-replacement fires. Late-successional species dominate when fire-return intervals are long, but historically fires were likely more frequent, preventing whitebark pine from being successional replaced. Although whitebark pine recruitment is depressed in many areas, whitebark pine seedlings were historically highly competitive with other conifer species in the post-fire environment. Emergence is best on burned and mineral soils. Fire reduce competition, giving seedlings in burn areas the best chance of growing into mature trees. Secondary succession, accelerated by white pine blister rust and bark beetle outbreaks, results in rapid replacement of whitebark pine by shade-tolerant, fire-sensitive species such as subalpine fir and mountain hemlock. Without burning, genetically valuable seed produced by blister-rust resistant whitebark pine is wasted as no new openings are created where Clark's nutcracker can cache seed and seedlings can establish. Augmenting natural regeneration with blister-rust resistant seed sources is recommended in areas where whitebark pine seed sources are absent or greatly reduced.

Rocky Mountain Lodgepole Pine

Lodgepole pine is susceptible to fire, mostly due to thin bark. However, mature lodgepole pine can survive patchy, low-severity fire under light fuel conditions if the fire does not completely char the circumference of the bole. Lodgepole pine bark is generally thin (approximately 0.25"

thick at most) and does not thicken appreciably with growth. Any bark charring is indicative of underlying dead cambium (Hood et al. 2008). Lodgepole pine trees develop thin, narrow crowns with a moderately low and open branch habit. Lower branches self-prune in dense stands; however, dead branches may persist on trees for several years.

Lodgepole pine begins producing seed, which may be borne in serotinous or nonserotinous cones, within 5 to 15 years of establishment. Individuals have predominately open or closed cones, and both cone types occur in single stands. Lodgepole pine is generally a prolific seed producer with good crops at 1- to 3- year intervals and light crops in intervening years. The average serotinous cone remains on the tree for about 15 years, with few remaining on a tree for more than 30 years. It is the accrual of cones on the tree over time (i.e., canopy seed banking) that results in large numbers of seed available for regeneration following disturbance. Serotinous cones require high temperatures to open and release seed, and they are well insulated to survive brief periods in flames. Serotinous cones are an adaptation to stand-replacing fire, and the seed supply is nearly always available on the tree. Crown fires usually cause maximum release of stored seed. However, crown fire that consumes cones may also consume or kill most of the seed stored in the canopy, regardless of serotinous cones. While lodgepole pines are easily killed by fire, they still provide an abundant seed supply. Other characteristics that contribute to lodgepole pine success and site dominance following fire are early seed production, prolific seed production, high seed viability, high seedling survival, and rapid growth. Lodgepole pine seeds are small and disperse easily with wind. Dispersal is based on cone serotiny. In stands with predominantly serotinous cones, releasing and scattering seed on the forest floor after fire opens cones is the most important method of dispersal. In stands with primarily nonserotinous cones, the small, winged seeds are dispersed largely by wind. Seedfall drops off rapidly as distance from source increases, with most seeds falling within about 200 feet of the parent tree. Lodgepole pine typically produces a substantial amount of regeneration after fire. Under favorable moisture conditions, lodgepole pine germinates best on exposed mineral soil. Fire creates a favorable seedbed by consuming litter and duff and also reduce competing vegetation, improving opportunities for seedling establishment. The decrease in canopy cover following fire provides high light intensity necessary for vigorous lodgepole pine seedling growth.

Western Hemlock

Western hemlock has low fire resistance. It has thin bark, shallow roots, highly flammable foliage, and a low-branching habit which makes it very susceptible to fire. The bark is thin (1 to 1.5") even on large trees. Any bark charring is indicative of underlying dead cambium (Hood et al. 2008). Western hemlock is shallow rooted and does not develop a taproot. The roots, especially fine roots, are most abundant near the surface and are easily damaged by fire. Even light ground fires are damaging because the shallow roots are killed. Western hemlock tends to form dense stands and its branches are often lichen covered, which further increases its susceptibility to fire damage. Post-fire mortality of western hemlock is common due to fungal infection of fire-caused wounds.

Like grand fir, in areas of low-intensity burns, hemlock that are not immediately killed by fire can produce a substantial amount of seed before dying that serves as a seed source for natural regeneration. Western hemlock is generally a good cone and seed producer. Cones may form on open-grown trees that are less than 20 years old, but good cone crops usually do not occur until

trees are between 25 and 30 years old. Individuals usually produce some cones every year and heavy cone crops every 3 or 4 years. Western hemlock seeds remain viable only into the first growing season after seedfall. Western hemlock seeds have large wings, enabling them to be distributed over long distances. In open, moderately windy areas, most seeds fall within 1,968 feet of the parent tree. Some seeds can travel as far as 3,772 feet under these conditions. In dense stands, most seeds fall much closer to the base of the parent tree. Western hemlock seed germinates well and seedlings grow well on almost all natural seedbeds if conditions are moist, whether rotten wood, undisturbed bed duff and litter, or bare mineral soil. Mineral soil is best for hemlock seedlings under drier conditions.

Engelmann Spruce

Engelmann spruce is easily killed by fire because it has thin bark that provides little insulation for the cambium, shallow roots which are susceptible to soil heating, low-growing branches, a tendency to grow in dense stands, moderately flammable foliage, and heavy lichen growth. Engelmann spruce is very susceptible to ground fires because fine fuels and duff under mature trees burns slowly and can girdle the thin-barked bole and kill the shallow roots. Bark charring is a reliable indicator that the underlying cambium is dead (Hood et al. 2008). Some large Engelmann spruce may survive light, patchy surface fires, but these often die later due to infection by wood-rotting fungi that enter through fire scars. Once fire damages the roots or boles of spruce, this species becomes very prone to windthrow and breakage (Alexander 1987). The fuel structure in stands dominated by Engelmann spruce and subalpine fir promotes high severity fires. The needles are small and fine, and form a compact fuel bed in which fire spreads slowly, which results in long residence times and high soil heating. Engelmann spruce's low-growing, lichen-draped branches often extend to the ground, making it easy for crown fires to start.

Engelmann spruce can begin producing cones when 15 to 40 years old and 4 to 5 feet tall, but under closed forest conditions seed production is generally not significant until trees are older and taller. Within natural stands, most seed is produced by dominant trees greater than 15" DBH. Although yearly production is erratic, Engelmann spruce is considered a moderate to good seed producer. Seed is generally dispersed within 300 feet by wind; when bumper seed crops occur, about 5 to 10 percent of the seed may be dispersed as far as 600 feet. Seeds overwinter under snow and germinate 2 to 3 weeks following snowmelt. Post-fire Engelmann spruce seedling establishment is best on moist surfaces where fire has consumed most or all of the duff leaving bare mineral soil. Seedlings do require some shade to survive; thus regeneration after fire is best on sites where standing dead trees, logs, or vegetation is present.

Subalpine Fir

Subalpine fir is one of the least fire-resistant western conifers and is easily killed by even low intensity fires. It is very susceptible to fire because it has thin bark that provides little insulation for the cambium, shallow roots which are susceptible to soil heating, low-growing branches, a tendency to grow in dense stands, highly flammable foliage, and moderate to heavy lichen growth. Bark charring is a reliable indicator that the underlying cambium is dead (Hood et al. 2008). The fuel structure in subalpine-fir-dominated stands promotes highly intensity fires. Fuel loads in subalpine fir stands are greater than in lower elevation montane stands because the cool

and moist environment slows the decomposition of organic matter allowing fuels to accumulate more rapidly. Fuel beds tend to be irregular, with over twice as much fuel accumulating under the narrow-crowned trees as between them. The small, fine needles form a compact fuel bed in which fire spreads slowly, leading to long residence times and high soil heating. Flames easily reach subalpine fir's low-growing branches, making it easier to initiate a crown fire. Once a crown fire begins, it spreads easily because subalpine fir has a tendency to grow in dense stands and has highly flammable foliage. In subalpine habitats, scattered subalpine fir trees often escape fire because of discontinuous fuels, broken and rocky terrain, and the moist and cool environment. The occasional mature tree which survives fire, trees persisting in small, unburned pockets, and trees adjacent to burned areas provide seeds to colonize burned sites.

Subalpine fir is very shade tolerant and easily establishes under a closed canopy. Subalpine fir can begin producing cones when 20 years old and 4 to 5 feet tall, but under closed forest conditions seed production is generally not significant until trees are older and taller. Maximum seed production is by dominant trees between 150 and 200 years old. Yearly seed production is very erratic; good seed crops are produced every 3 to 5 years, with light crops or crop failures in between. Seeds remain viable for 1 year and are wind-dispersed. Studies in Colorado showed that about one-half of subalpine fir seeds dispersed into clearcuts fell within 100 feet of the clearcut's windward edge, while the remainder fell within 260 feet of the edge. Seeds overwinter under or in snow. This cold, moist stratification is required for germination. Germination begins in the spring a few days after snowmelt and is usually completed within a few weeks. Seedlings establish best on mineral soil seedbeds but will also establish on other surfaces including litter, duff, and decaying wood. Subalpine fir readily establishes on burned mineral soil seedbeds. Ash does not affect germination, but if it is deep, it can prevent a seedling's roots from reaching mineral soil. Although seedling establishment is often favored by shade, it will establish in full sunlight following fire.

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