Pinus albicaulis Engelm. Whitebark Pine

Pinaceae Pine Family

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Whitebark pine (*Pinus albicaulis* Engelm.) is a slow-growing, long-lived tree of the high mountains of southwestern Canada and western United States. It is of limited commercial use, but it is valued for watershed protection and esthetics. Its seeds are an important food for grizzly bears and other wildlife of the high mountains. Concern about the species has arisen because in some areas whitebark pine cone crops have diminished as a result of successional replacement and insect and disease epidemics *(6,48)*.

Habitat

Native Range

Whitebark pine (fig. 1) grows in the highest elevation forest and at timberline. Its distribution is essentially split into two broad sections, one following the British Columbia Coast Ranges, the Cascade Range, and the Sierra Nevada, and the other covering the Rocky Mountains from Wyoming to Alberta.

Whitebark pine is abundant and vigorous on the dry, inland slope of the Coast and Cascade Ranges. It is absent from some of the wettest areas, such as the mountains of Vancouver Island. In the Olympic Mountains, it is confined to peaks in the northeastern rain shadow zone. Whitebark pine also occurs atop the highest peaks of the Klamath Mountains of northwestern California.

The Rocky Mountain distribution extends along the high ranges in eastern British Columbia and western Alberta, and southward at high elevations to the Wind River and Salt River Ranges in west-central Wyoming.

A small outlying population of whitebark pine is found atop the Sweetgrass Hills in north-central Montana 145 km (90 mi) east of the nearest stands in the Rocky Mountains across the Great Plains grassland (73).

The coastal and Rocky Mountain distributions lie only 100 km (62 mi) apart at their closest proximity *(10)*. Even this narrow gap is not absolute; small groves are found on a few isolated peaks in between in northeastern Washington. In addition to the main distribution, whitebark pine grows in the Blue and Wallowa Mountains of northeastern Oregon and in several isolated ranges rising out of the sagebrush steppe in northeastern California, south-central Oregon, and northern Nevada.

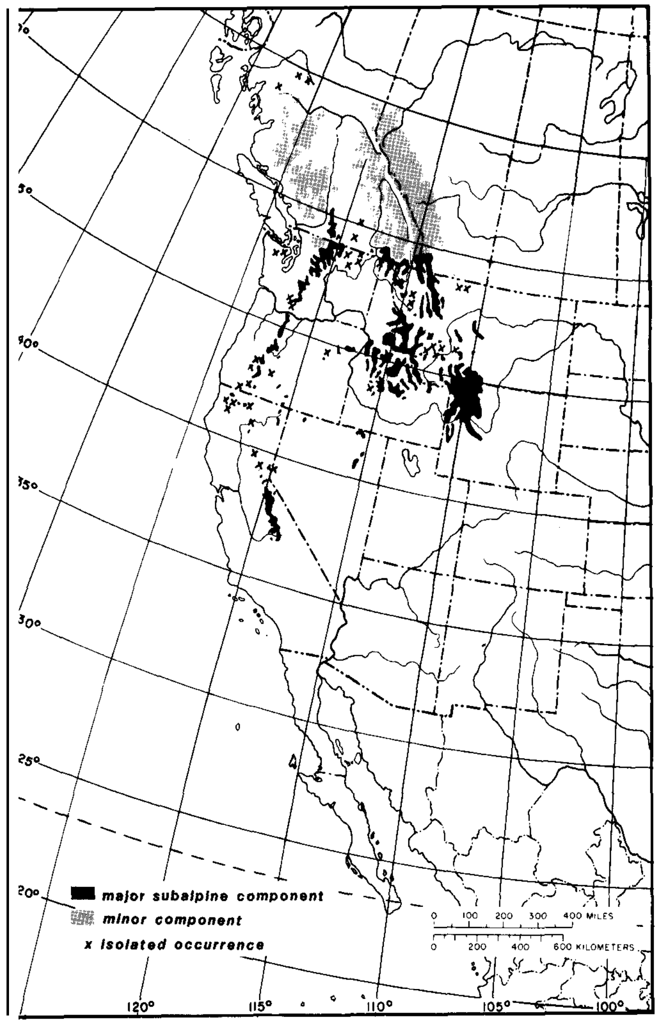

Figure 1-Natural *distribution of whitebark pine, revised from Little (53).*

Climate

Whitebark pine grows in a cold, windy, snowy, and generally moist climatic zone. In moist mountain

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ranges, whitebark pine is most abundant on warm, dry exposures. Conversely, in semiarid ranges, it becomes prevalent on cool exposures and moist sites. Weather data from several whitebark pine sites in the Inland Northwest suggest the climatic interpretations that follow (3,831. Summers are short and cool with mean July temperatures ranging from 13” to 15” C (55” to 59” F) in the whitebark pine forest and from 10” to 12” C (50” to 54” F) in the adjacent timberline zone. A cool growing season, as defined by mean temperatures higher than 5.5” C (42” F) *(11),* lasts about 90 to 110 days in the whitebark pine forest, but light frosts and snowfalls sometimes occur even in mid-summer. The hottest summer days reach temperatures of 26” to 30” C (79” to 86” F). January mean temperatures range from about -9” C (15” F) in Montana to about -5” C (23” F) in the Cascades and Sierra Nevada. Long-term record low temperatures in Montana and Wyoming stands are probably -40” to -50” C (-40” to -58” F).

Mean annual precipitation for most stands where whitebark pine is a major component probably is between 600 and 1800 mm (24 and 72 in). The lower part of this precipitation range applies to mountain ranges in semiarid regions where whitebark pine forms nearly pure stands or is accompanied only by lodgepole pine *(Pinus contorta* var. *latifolia).* The highest precipitation occurs in inland-maritime ranges and near the Cascade crest where whitebark pine grows primarily with subalpine fir *(Abies lasiocarpa)* and mountain hemlock *(Tsuga mertensiana).*

About two-thirds of the precipitation in most stands is snow and sleet, with rain prevailing only from June through September (3). Summer rainfall is often scant in the southern part of whitebark pine's distribution south of about 47” N. latitude. Thus, there is often a droughty period with scant rainfall or remaining snowmelt water for several weeks during mid- to late-summer.

Snowpack usually begins to accumulate in late October. By April, the snowpack reaches maximum depth, ranging from about 60 to 125 cm (24 to 50 in) in stands east of the Continental Divide and in other semiarid areas, to 250 to 300 cm (100 to 120 in) in the relatively moist whitebark pine-subalpine fir stands of the Cascades and inland-maritime mountains. Most stands probably have mean annual snowfalls between 460 and 1270 cm (180 and 500 in). Whitebark pine also grows in stunted or krummholz (shrub-like) form on windswept ridgetops where little snow accumulates.

Strong winds, thunder storms, and severe blizzards are common to whitebark pine habitats. Wind gusts of hurricane velocity in the tree crowns (more than 117 km/h or 73 mi/h) occur each year on most sites, but most frequently on ridgetops.

Soils and Topography

Most whitebark pine stands grow on weakly developed (immature) soils. Many of the sites were covered by extensive mountain glaciers during the Pleistocene and have been released from glacial ice for less than 12,000 years (62). Chemical weathering is retarded by the short, cool, summer season. Also, nitrogen-fixing and other microbiotic activity that might enrich the soil is apparently restricted by low soil temperature and high acidity on many sites.

Despite these general trends, substantial variations occur in local climates, geologic substrates, and degrees of soil development in whitebark pine habitats. Thus, several types of soils have been recognized.

Most soils under whitebark pine stands are classified as Inceptisols (82). Many of these are Typic Cryochrepts, although deposits of volcanic ash may be sufficiently thick in some profiles to warrant recognition as Andic Cryochrepts. Some of the best-developed, ash-layered soils beneath spruce-fir–whitebark pine stands are Typic Cryandepts similar to the zonal Brown Podzolic soils (64). All of these are young soils, showing less leaching, weathering, and horizon development than Spodosols, although they are strongly acidic. Mean pH values of 4.8 to 5.0 were found for the upper mineral soil horizons in three habitat types, probably composed largely of Typic Cryochrepts (66). Data on nutrient availability in these soils have been provided (83).

Throughout its distribution, whitebark pine is often found on soils lacking fine material. Sparse open stands often grow on coarse talus, exposed bedrock, or lava flows having minimal horizon development and only scattered pockets of fine material. These soils would be classified as fragmental and loamy skeletal families within the order Entisols (Cryorthents in granitic substrates) *(82).* They have been referred to as azonal soils, and more specifically as Lithosols in earlier classifications.

Some dry-site whitebark pine stands in semiarid regions have open, grassy understories, particularly on calcareous rock substrates. The soils have a thick, dark surface horizon and a nearly neutral reaction. The pH is near 6 in Montana (66) and Idaho *(71)* stands, but in Alberta average values are 7.8 to 8 *(9).* These soils would evidently be classified as Typic Cryoborolls within the order Mollisols (82). Also, in some of the same areas, soils that have a dark surface but low base saturation are classified as Typic Cryumbrepts.

In all but the driest regions, whitebark pine is most abundant on warm aspects and ridgetops having direct exposure to sun and wind. It is less abundant on sheltered, north-facing slopes and in cirque basins, where subalpine fir, Engelmann spruce *(Picea engelmannii),* mountain hemlock, or alpine larch ***(Larix lyallii)*** become prevalent. Nevertheless, the tallest and best formed whitebark pine trees are, often found in high basins or on gentle north slopes.

Near the northern end of its distribution in the British Columbia coastal mountains, whitebark pine is a minor component of timberline communities at about 1580 m (5,200 ft) elevation (58). In the Olympic Mountains and on the western slope of the Cascades in Washington and northern Oregon, it grows primarily on exposed sites near tree line between 1770 and 2130 m (5,800 and 7,000 ft). (Elevational ranges mentioned are mostly from 7). East of the Cascade crest it becomes abundant within both the subalpine forest and the timberline zone. For instance, it is common between 1620 and 2440 m (5,300 and 8,000 ft) in central Washington's Stuart Range, generally forming krummholz above 2130 m (7,000 ft). The lowest reported natural stand of whitebark pine throughout its range is at 1100 m (3,600 ft) near Government Camp on the southwest slope of Mount Hood in Oregon (28).

Whitebark pine becomes a major component of high-elevation forests in the Cascades of southern Oregon and northern California, growing between 2440 and 2900 m (8,000 and 9,500 ft) on Mount Shasta. In the central and southern Sierra Nevada it is found between 3050 and 3510 m (10,000 and 11,500 ft) but occasionally reaches 3660 m (12,000 ft) as krummholz cushions.

Near the north end of its distribution in the Rockies of Alberta and British Columbia, whitebark pine is generally small, scattered, and confined to dry, exposed sites at timberline, 1980 to 2290 m (6,500 to 7,500 ft). It becomes increasingly abundant southward, especially in Montana and central Idaho. It is a major component of high-elevation forests and the timberline zone between about 1800 and 2500 m (5,900 and 8,200 ft) in northwestern Montana and 2130 and 2830 m (7,000 and 9,300 ft) in west-central Montana. In western Wyoming, it is abundant at 2440 to 3200 m (8,000 to 10,500 ft).

Associated Forest Cover

Whitebark pine is most frequently found growing with other high mountain conifers, although pure whitebark pine stands are common in dry mountain ranges. The forest cover type Whitebark Pine (Society of American Foresters Type 208) (70) is used to designate pure stands or mixed stands in which the species comprises a plurality. Whitebark pine is also a minor component of Engelmann Spruce-Subalpine Fir (Type 206) in the Rockies, eastern Cascades, and the Blue Mountains; Mountain Hemlock (Type 205) in much of the Cascades and British Columbia coastal mountains; and California Mixed Subalpine (Type 256) in the California Cascades, Sierra Nevada, and Klamath Mountains. In these open, upper subalpine forests, whitebark pine is associated with mountain hemlock, California and Shasta red fir ***(Abies magnifica*** vars. ***magnifica*** and ***shastensis),*** Sierra lodgepole pine *(Pinus contorta* var. ***murrayana),*** western white pine *(P. monticola),* and locally, foxtail *(P. balfouriana)* and limber *(P. flexilis)* pines.

In the dry ranges of the Rockies south of latitude 47° N. and in south-central Oregon, whitebark pine is found within the highest elevations of the cover type Lodgepole Pine (Type 218). In the Rockies, whitebark pine adjoins Interior Douglas-Fir (Type 210) and Limber Pine (Type 219). In the East Humboldt, Ruby, Jarbidge, and Bull Run Ranges of northeastern Nevada, whitebark's principal associate is limber pine (23).

In the timberline zone, conditions for tree development are so severe that any species that can become well established is considered a part of the climax community. In Montana and northern Idaho, the whitebark pine stands in the timberline zone (above forest line or where subalpine fir becomes stunted! make up the *Pinus albicaulis–Abies* ***Zasiocarpa*** habitat types *(24,66).* Whitebark pine is also a climax species in other habitat types, mostly on dry sites, in Montana, central Idaho, and western Wyoming *(71,72,83). Pinus albicaulis /* ***Vaccinium scoparium*** is probably the most widespread and abundant habitat type that includes pure whitebark pine stands in the Rocky Mountains. Various aspects of the ecology of this habitat type in Montana and Wyoming have been described *(26,27,83).*

In the subalpine forest of the Northern Rockies whitebark pine is a principal long-lived seral component of the ***Abies** lasiocarpa / Luzula* ***hitchcockii*** and ***Abies** lasiocarpa–Pinus albicaulis / Vaccinium* ***scoparium*** habitat types (66). Prior to the early 1900's, whitebark pine was apparently more abundant in the subalpine forest as a result of natural fires, which favored its survival and regeneration over competing fir and spruce *(6,46,63).* In the southern Canadian Rockies and the inland mountains of southern British Columbia, whitebark pine is also primarily a seral associate in the highest elevations of the subalpine fir-spruce forest *(1,9,65).*

Principal undergrowth species in Rocky Mountain and northern Cascade stands include grouse whortleberry *(Vaccinium scoparium),* mountain arnica *(Arnica latifolia),* red mountain heath *(Phyllodoce empetriformis),* rustyleaf menziesia *(Menziesia ferruginea),* smooth woodrush *(Luzula hitchcockii),* beargrass *(Xerophyllum tenax),* elk sedge *(Carex geyeri),* Parry rush *(Juncus parryi),* Ross sedge *(Carex rossii),* and Idaho fescue *(Festuca idahoensis).* In south-central Oregon the primary undergrowth species are long-stolon sedge *(Carex pensylvanica)* and Wheeler bluegrass *(Poa nervosa)* (41). Undergrowth is sparse in Sierra Nevada stands.

Life History

Reproduction and Early Growth

Flowering and fruiting-Whitebark pine is monoecious. The female strobili and cones develop near the tip of upper crown branches while the male or pollen strobili develop throughout the crown on the current year's growth *(10,60).* Whitebark pine flowers are receptive and pollen is shed during the first half of July, but at some mid-elevation sites the species probably flowers in June. The ripe pollen strobili are a distinct carmine, which distinguishes them from the yellow pollen strobili of limber pine. The importance of various factors limiting pollination and fertilization is unknown. The isolation of some individual trees and small populations planted by birds, such as Clark's nutcracker, may prevent pollination. Also, animal planting of genetically similar seeds in a given area might increase the level of inbreeding, which might reduce regeneration success.

The female or seed cones ripen by early September of the second year *(81).* Although there are no good exterior signs of cone and seed ripeness, the cone scales open slightly-but not enough to release the seeds-and can be pulled apart after September 1.

Seed Production and Dissemination-Large seed crops are produced at irregular intervals, with smaller crops and crop failures in between. Cone crops may be produced more frequently in the southern parts of whitebark pine's distribution *(10).* In a Sierra Nevada study area, whitebark pine cone crops were moderate to heavy in each of four years, 1973 to 1976 (74). A study of 29 whitebark pine stands in the northern Rockies found that cone production averaged about 14,000 per hectare (6,000 per acre) over an 8-year period (84). Seeds number from 4,850 to 9,900/kg (2,200 to 4,500/lb) *(60,81).*

The large, heavy, wingless seeds are borne in dense, fleshy, egg-shaped cones usually 5 to 8 cm (2 to 3 in) long. The cone is dark purple, turning brown as it cures in late summer. It is unusual among cones of North American pines in remaining essentially closed (indehiscent) after ripening rather than spreading its scales to release seeds (75). Most of the cones are harvested by animals. Some fall to the ground where they disintegrate rapidly by decay and depredations by mammals and birds. A small percentage remain on the tree into winter. A few cones, complete with weathered scales but without seeds, remain on the branches for several years after ripening.

Clark's nutcrackers and red squirrels attack most of the ripening cone crop in the tree tops during August and September. As a result, it is common to find no evidence of cones in a whitebark pine stand except when a careful search is made for cone scales on the ground *(10).*

Clark's nutcrackers have an essential role in planting whitebark pine seeds *(42,49,51,74,76,77).* Nutcrackers can carry as many as 150 whitebark pine seeds in their sublingual (throat) pouch and they cache groups of one to several seeds in the soil at a depth of 2 to 3 cm (1 in), suitable for germination. Nutcrackers cached an estimated 33,600 limber pine seeds per hectare (13,600/acre) in one open, burned area during one summer; a similar pattern of seed caching would be expected for whitebark pine. Whitebark pine seeds sustain these birds and their young much of the year, but a large proportion of the seed caches go unrecovered.

The effects of whitebark pine seed planting by Clark's nutcrackers are readily observable. Despite its heavy wingless seed, this species often regenerates promptly on burned or clearcut areas where a seed source is absent *(46,59,76,77,78).* Moreover, whitebark pine seedlings in open areas frequently arise together in tight clumps of two to five. The species has become established atop a young geologic formation-Wizard Island in Crater Lake, Oregon, *(43)*—where seed dispersal by birds would have been necessary. Lone whitebark pine trees grow along alpine ridges, often several miles from the nearest possible seed source (7). Numerous clumped whitebark pine seedlings and saplings can be found far from a seed source in lower elevation forests (for example with ponderosa pine), where whitebark pine does not develop beyond sapling stage. Clark's nutcrackers migrate down to these stands in autumn, bringing whitebark pine seeds with them *(7,74).*

Various mammals also transport and cache whitebark pine seeds *(42,74).* Red squirrels harvest large quantities of whitebark pine cones and store them in rotten logs and on the ground. Black and grizzly bears raid many of these cone caches, scattering many seeds. Chipmunks, golden-mantled ground squirrels, and deer mice eat loose seeds and also cache seeds that may ultimately germinate. Red squirrels also cache whitebark pine seeds; from 3 to 176 seeds per cache have been found (47).

A few seeds probably fall onto favorable seedbeds near the parent trees. Rarely, seeds may be carried by snow avalanches into lower elevations. Because of periodic disturbances and cold air drainage in avalanche chutes, whitebark pine saplings often occupy these sites at low elevations. Presumably, most of these trees arise from nutcracker caches.

The poor germination rate (8 to 14 percent) of whitebark pine seed under field conditions is apparently related to the development and condition of the embryo and to seed coat factors (60). Seeds from three Canadian sources germinated poorly, despite a variety of seed coat scarification techniques with and without cold stratification (68). The best results were obtained when a small cut was made in the heavy seed coat and the seed was placed adjacent to germination paper to facilitate water uptake. The seed coat is evidently a major cause of delayed regeneration or seed dormancy. Another factor explaining the low germination was the low proportion of seeds with fully developed embryos. In another test, using seed collected from Idaho, 61 percent of the seed germinated after clipping of the seed coat (67). Stratification for 60 days plus clipping resulted in 91 percent germination. Cold stratification for at least 150 days followed by cracking of the seed coat has been fairly successful, resulting in 34 percent germination (37).

Seedling Development-Germination is epigeal *(81).* The newly germinated seedlings of whitebark pine are large compared with other mountain conifers. Cotyledons number 7 to 9 *(36),* and while still in the cotyledon stage, the seedlings are 8 to 10 cm (3 to 4 in) tall, with a 13 to 18 cm (5 to 7 in) taproot *(25).*

Vegetative Reproduction-Unlike associated subalpine fir, Engelmann spruce, and mountain hemlock, whitebark pine spreads only to a minor extent through layering-rooting of lower branches that are pressed against moist ground. At the upper elevational limit of tree growth, whitebark pine forms islands of shrub-like growth (flagged krummholz and cushion krummholz, fig. 2), similar in general appearance to the layered krummholz of fir and spruce described by Marr (55). A recent inspection of whitebark pine krummholz in the Montana Bitterroot Range confirmed that layering occurs *(5).* Investigation revealed that much of the spread of an individual krummholz plant results from branches extending horizontally from a central point, but also that in some plants these long branches become pressed into the surface soil and have developed large roots, which clearly constitutes layering.

Whitebark pine is easily grafted on rootstock of either whitebark pine or western white pine. The grafts grow much faster when the stock plant is western white pine (44).

Sapling and Pole Stages to Maturity

Growth and Yield-Whitebark pine is a slow-growing, long-lived tree. It can attain small to moderately large size after 250 or more years depending on site conditions. Growth and yield information on this species is scarce because it is of little interest for commercial timber production. Occasionally, old growth whitebark pine makes up a modest proportion of the timber harvested on moist, high-elevation sites.

In Montana, the best sites for whitebark pine timber growth are generally in the *Abies lasiocarpa / Luzula hitchcockii* habitat type, *Menziesia ferruginea* phase (66). Although whitebark pines of good form and moderately large size [dominant trees 50 to 75 cm (20 to 30 in) in d.b.h. and 21 to 30 m (70 to 100 ft) tall at 250 to 300 years of age1 sometimes develop on these sites, associated Engelmann spruce grows larger and is the primary object of management. In some commercial forest sites between 1520 and 1830 m (5,000 and 6,000 ft) in southwestern Alberta, whitebark pine grows larger than associated lodgepole pine and spruce *(25).* In south-central Oregon, annual yields of merchantable timber in a lodgepole pine-whitebark pine type were estimated to be about 2.0 m^3/ha (29 ft^3/acre) *(41).*

On the best sites, where whitebark pine is a component of the spruce-subalpine fir forest, it produces timber of good quality with only a moderate amount of defect. The resulting lumber has properties similar to those of western white pine (45) but is graded lower largely because of its slightly darker appearance (85).

At higher elevations where the species is abundant, it forms a short tree with large branches and is unsuitable for timber production. Detailed information on productivity in some of the pure, high-elevation whitebark pine stands-Pinus albicaulis/Vaccinium scoparium habitat type-suggests that annual yields of merchantable timber are low, about 0.7 to 1.4 m^3/ha (10 *to 20* ft^3/acre) *(27,83,66).*

Figure 2—*Whitebark pine near timberline with typical upswept, branched crown.*

On favorable sites near the forest line, this species develops into a large, single-trunk tree commonly 11 to 20 m (35 to 65 ft) tall and has a life span of 500 years or more. The oldest individuals on some cold, dry sites probably attain 1,000 years. The ancient trees often have a broad crown composed of large ascending branch-trunks (fig. 3). The largest recorded whitebark pine, growing in central Idaho's Sawtooth Range, is 267 cm (8 ft 9 in) in d.b.h. and 21 m (69 ft) tall (2). Upwards through the timberline zone, whitebark pine becomes progressively shorter and assumes multi-stemmed growth forms (fig. 4), evidently arising from the germination of nutcracker seed caches *(30,52)*. Because seeds in these caches often come from the same tree, the individual trees that make up a single multi-stemmed tree are often siblings. As a result, tree "clumps" may be composed of individuals more closely related to one another than to adjacent clumps.

At its upper limits, whitebark pine is reduced to shrublike growth forms (fig. 2) *(20)*. Such krummholz stands are often extensive on wind-exposed slopes and ridgetops. Primary causes of krummholz are thought to be inadequate growing season warmth, which prevents adequate growth, maturation, and hardening (cuticle development) of new shoots *(79)*. As a result, shoots are easily killed by frost or by heating and desiccation on warm sunny days in early spring when the soil and woody stems are frozen and thus little water is available to replace transpiration losses. Mechanical damage from ice particles in the wind is also a factor limiting krummholz growth to microsites where snowpack accumulates and provides protection from sun and wind.

Rooting Habit-On most sites, whitebark pine develops a deep and spreading root system. It is well anchored into the rocky substrate and is seldom uprooted despite its large, exposed crown and the violent winds to which it is subjected. Lanner *(50)*, however, observed shallow rooting that allowed windthrow in whitebark pines growing on moraines in Wyoming. These trees had pancake like root systems only 40 cm (16 in) deep. Shallow rooting probably occurs also where the species inhabits high-elevation bogs.

Reaction to Competition-Although whitebark pine has been tentatively rated very intolerant of competition or shade *(12)*, recent observers *(8,25,60,66,71)* believe that it is intermediate or intolerant, about equivalent to western white pine or interior Douglas-fir. Whitebark pine is less tolerant than subalpine fir, spruce, and mountain hemlock; however, it is more tolerant than lodgepole pine and alpine larch. In moist, wind-sheltered sites where spruce, fir, or hemlock are capable of forming a closed stand, whitebark pine can become a long-lived seral dominant in the aftermath of fires, snow avalanches, or blowdowns.

On a broad range of dry, wind-exposed sites, whitebark pine is a climax or near-climax species that persists indefinitely in association with subalpine fir and other tolerant species because it is hardier, more drought tolerant, more durable, and longer-lived. Even on these severe sites, however, a successional trend may be observable on a small scale: whitebark pine pioneers on an open site and is later surrounded and locally replaced by tolerant fir and hemlock (29). In dry areas of Wyoming's Wind River and in south-central Oregon, whitebark pine forms a co-climax with lodgepole pine in dense subalpine forest stands (41,721.

Observations of whitebark pine natural regeneration suggest that this species could be perpetuated on dry sites under a variety of even-aged or uneven-

Figure *3-Multi-stemmed growth form of whitebark pine at treeline in northeastern Olympic Mountains, WA.*

aged silvicultural systems. To establish whitebark pine on moist sites, some stand opening and light, localized site preparation are probably necessary. Wind-throw and wind breakage are a danger to residual trees, especially spruce and fir, in partial cuttings. Watershed values (and often esthetic values) are high on whitebark pine sites, however, and use of heavy equipment could be damaging. Whitebark pine can be regenerated by outplanting seedlings, or sowing seeds in mineral soil or at the soil-litter interface *(60).*

Damaging Agents-Mountain pine beetle ***(Dendroctonus ponderosae)*** is by far the most damaging insect in mature stands of whitebark pine ***(13).*** Much of the mature whitebark pine in the northern Rockies was killed by this insect between 1909 and 1940 *(3,19,31).* Epidemics evidently spread upward into the whitebark pine forest after becoming established in the lodgepole pine forests below. In the 1970's, an epidemic developing in lodgepole pine in the Flathead National Forest of Montana killed most of the whitebark pine in some areas. This insect usually kills only the larger whitebark pine trees because such trees have an inner bark layer thick enough for the larvae to inhabit. Small trees are also killed in areas of intense infestation.

Less damaging insect infestations are caused by aphids ***(Essigella gillettei)*** that feed on needles, mealybugs ***(Puto cupressi*** and ***P. pricei)*** that feed on trunks and branches, and the lodgepole needletier ***(Argyrotaenia tabulana),*** a potentially destructive defoliator. At least one species of Ips, the Monterey pine Ips ***(Ips mexicanus),*** infests the bole, and ***Pityogenes carinulatus*** and ***P. fossifrons*** also infest the bole ***(31). Two*** species of ***Pityophthorus (P. aquilonius*** and ***P. collinus)*** have been collected from whitebark pine ***(18).*** The ponderosa pine cone beetle ***(Conophthorus ponderosae)*** infests cones of whitebark pine (86).

The principal disease is the introduced white pine blister rust (caused by ***Cronartium ribicola) (38).*** Blister rust is particularly destructive where the ranges of whitebark pine and blister rust coincide with good conditions for infection. This occurs where adequate moisture permits infection of local ***Ribes*** spp. (currant and gooseberry bushes, the rust's alternate hosts) in early summer and prevents drying of the infected ***Ribes*** leaves throughout the summer. Where there is a source of inoculum from lowland forests, the spores that infect pine can be carried by wind to the trees, but cool, moist conditions are needed for infection (14). Blister rust damage is severe and prevents tree development in some timberline areas of the northern Cascades, northern Idaho, and northwestern Montana where whitebark pine is the major pioneer species (48). (Resistance is discussed under "genetics".)

Several other diseases infect whitebark pine, generally with minor consequences *(34,35,69).* These diseases are stem infections that produce cankers (some similar to blister rust), such as ***Atropellis pinicola, A. piniphila, Lachnellula pini (Dasyscypha pini),*** and ***Gremmeniella abietina;*** a wood rot organism ***Phellinus pini;*** several root and butt rots caused by ***Heterobasidion annosum, Phaeolus schweinitzii,*** and ***Poria subacida;*** and several needle

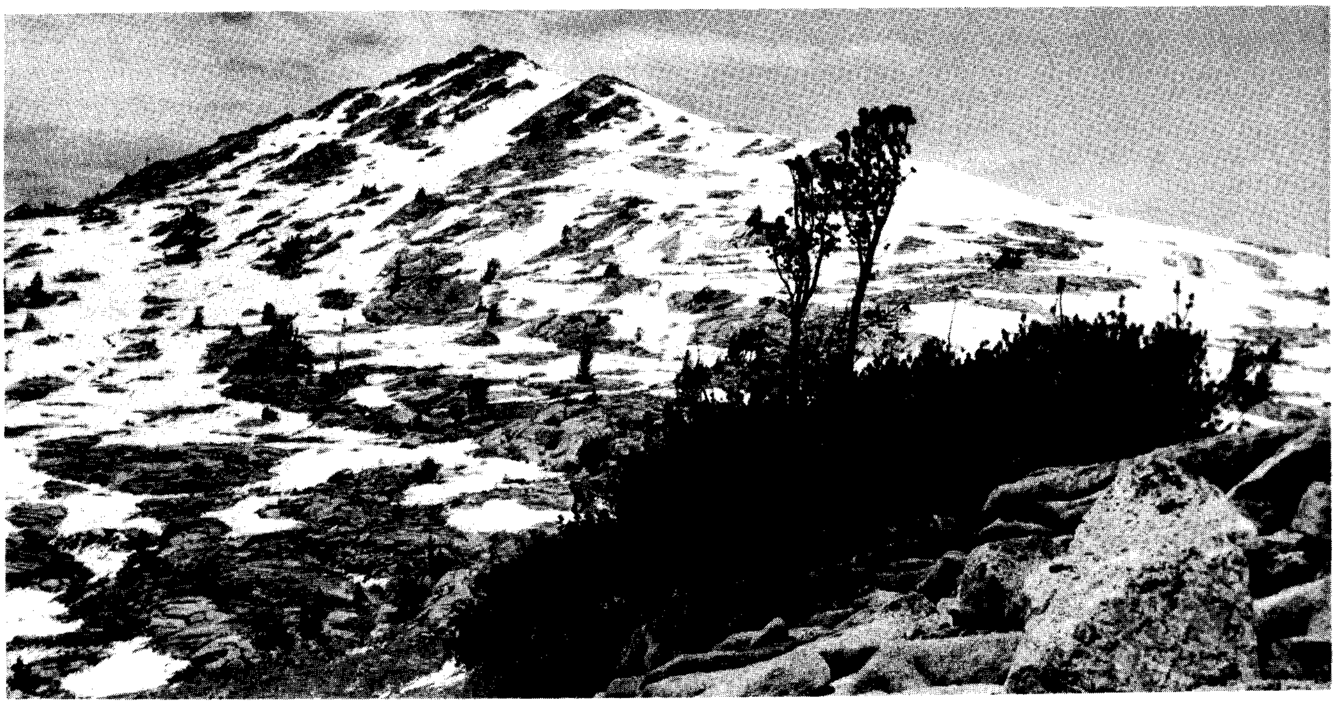

Figure 4—*Krummholz whitebark pine at 3230 m (10,600 ft) Granite Pass, Sequoia-Kings Canyon National Park, CA. The krummholz "cushion" is protected by winter snowpack; the wind-battered upper branches are called "flags."*

cast fungi including ***Lophodermium nitens, L. pinastri, Bifusella linearis,*** and ***B. saccata.*** When foliage is covered by snow for long periods, a snow mold, ***Neopeckia coulteri,*** appears (34,35,69).

The dwarf mistletoes (***Arceuthobium*** spp.) cause severe local mortality. The most widespread species is the limber pine dwarf mistletoe (***A. cyanocarpum***), which causes extensive damage to whitebark pine on Mount Shasta and some nearby areas of northern California (56). In the northern Rockies, the lodgepole pine dwarf mistletoe (***A. americanum***) occasionally occurs on whitebark pine where this tree grows in infested lodgepole pine stands. In the Oregon Cascades, the hemlock dwarf mistletoe (***A. tsugense***) is damaging to whitebark pine (33,56).

In addition to these parasitic organisms, several harmless saprophytes grow on whitebark pine: ***Lachnellula pini*** (***Dasyscypha agassizii***) on dead bark and cankers of blister rust, ***D. arida, Tympanis pinastri,*** and ***Phoma harknessii*** on twigs (34). ***Cenococcum graniforme*** has been identified as an ectotrophic mycorrhizal fungus of whitebark pine (80).

Wildfire is an important vegetation recycling force in whitebark pine stands, although long intervals (50 to 300 years or more depending on the site) usually occur between fires in a given grove (4). Lightning has been the major cause of fires in most stands; however, increased recreational use of forests results in accidental fires. Many of the fires have spread upslope into whitebark pine after developing in lower forests. Tiny spot fires are most common because fuels are generally sparse and conditions moist and cool. Nevertheless, occasional warm and dry periods accompanied by strong winds allow fires to spread. Spreading fires often remain on the surface and kill few large trees, but, under extreme conditions, severe wind-driven fires burn large stands (4). Wildfire (enhanced by fuels created by epidemics of ***Dendroctonus ponderosae*** in lodgepole and whitebark pine), followed by seed dissemination by Clark's nutcrackers, may be the principal means by which whitebark pine becomes established in the more productive sites near its lower elevational limits. Conversely, after a severe fire on dry, wind-exposed sites, regeneration of whitebark pine (often the pioneer species) may require several decades *(6,77).*

Wind breakage of the crowns or boles occurs when unusually heavy loads of wet snow or ice have accumulated on the foliage. This damage is prevalent in large, old trees having extensive heart rot. Snow avalanches also are an important damaging agent in some whitebark pine stands.

Special Uses

Whitebark pine's greatest values are for wildlife habitat, watershed protection, and esthetics. Seeds are an important, highly nutritious food source for many seed eating birds and small mammals, as well as for black bears and grizzly bears *(47,57,61).*

Blue grouse feed and roost in whitebark pine crowns during much of the year. This tree provides both hiding and thermal cover in sites where few if any other trees grow. The large, hollow trunks of old trees and snags provide homesites for cavity-nesting birds. The seeds of whitebark pine were occasionally used as a secondary food source by Native Americans *(17,54).*

Whitebark pine helps to stabilize snow, soil, and rocks on steep terrain and has potential for use in land-reclamation projects at high elevation (68). It provides shelter and fuel for hikers and campers and is an important component of the picturesque setting that lures hundreds of thousands of visitors into the high mountains (21).

Genetics

Most of the wide phenotypic growth form variation in whitebark pine is apparently the result of differences in site and climate. Krummholz whitebark pines have apparently arisen from nutcracker caches of seeds from erect trees *(77),* implying that the prostrate form is environmentally induced. Conversely, Clausen *(20)* hypothesized that the alpine (krummholz) and subalpine (tree) forms have a genetic basis. Determination of this will have to await genetic tests. Enzyme studies suggest that high-elevation forms of Engelmann spruce and subalpine fir do have a genetic basis *(32),* but another study showed that a prostrate form of the European stone pine *(Pinus cembra),* closely related to whitebark, can spontaneously produce an erect tree stem (40).

Resistance to white pine blister rust is the most notable phenotypic variation observed in whitebark pine. The species was extremely susceptible to blister rust both in the field and nursery in artificial inoculation tests and has been rated by many people as the most susceptible of all the world's white pines *(15).* In stands where mortality has been as high as 90 percent, however, many individuals have survived and some are free of rust symptoms. Genetic testing, using artificial inoculation methods to expose seedlings from uninfected wild parents, has demonstrated resistance to be genetic (38). Four main defense mechanisms were observed: absence of infections of needles or stem, shedding of infected needles before the fungus could reach the stem, a chemical interaction between the fungus and short-shoot tissue that killed the fungus, and chemical reactions in the stem that killed host cells, with subsequent walling off of the fungus.

A small trial plantation of first-generation wind-pollinated seedlings from resistant whitebark pine parents was established at Marks Butte near Clarkia, Idaho, in 1979 (37). A survey in 1989 revealed 10 surviving seedlings of 200 planted. The survivors were about 1 foot tall. Much of the mortality was due to vegetative competition, especially by bear-grass. Survival of planted resistant seedlings would provide a first step toward returning whitebark pine as an important component of the subalpine plant communities, where the adverse impact of birds and rodents on the rust-induced mortality is high and where remaining seed supply is great.

Many attempts have been made to cross whitebark pine with the other four white pine species in its subsection *Cembrae* and with most species in subsection *Strobi.* Almost all have ended in failure or inconclusive results *(16).* Only the cross with limber pine, from subsection *Strobi,* offers slight hope (22). No putative hybrids of whitebark pine have been identified in natural stands.

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